

POPULATION STRUCTURE IN SALT MARSH SONG SPARROWS
PART I. ENVIRONMENT AND ANNUAL CYCLE

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The Song Sparrows (*Melospiza melodia*) that live on the salt marshes of San Francisco Bay, California, have attracted the attention of students of birds for the past sixty years. The principal reason for this has been their morphological distinctness from all other Song Sparrows, including those that live in areas close to the salt marshes. Such a pattern of differentiation and distribution has always raised the problem of how the salt-marsh populations maintain themselves as distinct entities. The study reported now is a continuation of previous work on salt-marsh Song Sparrows; the questions asked were, what characteristics of salt-marsh populations influence or have some relationship to the maintenance of their morphologic and/or genetic integrity, and how do these characteristics express themselves?

Certain details bearing on these questions that are supplied in this and a succeeding paper have been interpreted in the light of the theoretical and factual framework partly supplied by such authors as Wright (1940; 1943), Mayr (1942; 1953), Miller (1947), and Marshall (1948).

The Song Sparrows studied exist partly isolated from other populations of Song Sparrows on San Pablo salt marsh, Richmond, Contra Costa County. They offered advantages not otherwise generally available to the worker in population ecology of birds: they were abundant and were situated in a discrete unit of salt marsh; they belonged to a group genetically distinctive to the extent of being accorded the taxonomic status of race (*M. m. samuelis*); they were non-migratory; they had been studied from a general ecological viewpoint by Marshall (*loc. cit.*); and they belonged to a widespread species for which Nice (1937; 1943) had compiled a definitive life history based on studies in Ohio. Thus, most of the effort in studying the birds was directed to the investigation of population structure. Since these Song Sparrows differ in certain respects from those in Ohio, a number of features of their life history that bear on population structure are included. I have not offered a comparison of these differences except where it has seemed to be particularly significant.

Generous help and counsel in the preparation of this report have been given me by Alden H. Miller, Frank A. Pitelka and Ray F. Smith; their suggestions have applied to all parts of the study. Responsibility for validity at all levels remains mine, however. The habitat photographs were taken by Joseph G. Hall. My wife, Lora Lee Johnston, assisted with preparation of manuscript. It is a pleasure to acknowledge the aid of these people.

METHODS

Trapping.—A variety of small bird traps, mostly of the Potter two-cell and Bailey collapsible types, constructed of hardware cloth were used in the trapping. Baits used were a variety of commercially available grains and "wild bird" seed mixtures. These were of low success in catching both juvenal and adult birds. Identical methods used in the uplands were highly successful in trapping Song Sparrows. Salt-marsh Song Sparrows do not come readily to traps baited with grain, probably due to their characteristic dietary preferences.

Nest-finding.—As a result of my inability to trap many Song Sparrows, special effort was made to find nests so that a large number of nestlings could be banded. This program was not as successful as it might have been, due primarily to the fact that the salt-marsh Song Sparrow does not have a "typical" nest site; it was therefore impossible to count on finding the nest of any specific pair. The principal method of finding nests

was to flush the incubating or sitting females from them. Rapid walking through territories was found to be best for this, for if the birds had sufficient warning of my presence, they would slip off the nest and run away over the ground surface; they would invariably never be seen in such instances (the fact that they did this was determined through observation at known nests). A few nests were found by observing the actions of the adults during the time that they were feeding nestlings and a few by prolonged search of all likely nesting sites in a given territory.

Banding.—Each bird was banded with a Fish and Wildlife Service aluminum, numbered band, plus plastic bands in a distinctive combination of colors. In the years from 1950 to 1953 I used coiled plastic strips that had to be fixed to the leg of the bird with the help of a drop of acetone base cement. In 1954–1955 I used split plastic bands of very high tensile strength. These were manufactured by the A. C. Hughes Company of Hampton Hill, England. These are especially useful on nestling birds, as they require no cementing and are affixed rapidly. A total of 287 birds was banded; of this number 241 were nestlings, 33 adults, and 13 juveniles.

Censusing.—Censuses of salt-marsh Song Sparrows may be made accurately only in the breeding season. At other time of the year the birds are, as a population, hard to see, preferring to stay in heavy cover of vegetation or in slough bottoms in the shadows. My records for all birds have gaps that represent periods of time during which it was not possible to find them. Some of the gaps are as long as one year; I have always assumed that a bird that returned but had been missing was not gone from the area but merely escaped my notice.

Marshall (1948:196) described the method of counting in the breeding season: one merely walks the length of a tidal slough and marks off on a map of that slough the occurrence of territorial males or pairs, as the case may be. One such count would be enough for most analyses, but I do not have less than two formal counts for individual sloughs in one season. Numerous additional checks of restricted parts of sloughs were made in the course of the nesting season as a result of other field activities.

ENVIRONMENT

Locality.—San Pablo salt marsh lies about one mile north-northwest of the center of the city of Richmond. This marsh has its front on San Pablo Bay, the northernmost part of San Francisco Bay. The bay at this point in Contra Costa County is shallow for hundreds of yards offshore; at low water about 1000 yards of mudflat is exposed off San Pablo marsh and for yet another mile the water is but four feet deep. Depths of 60 to 80 feet are reached only in the channel, cut during the last Glacial Period by the Sacramento-San Joaquin River.

San Pablo marsh is typical of relatively undisturbed San Francisco Bay salt marsh (see Marshall, 1948:205; Hinde, 1954), being composed primarily of two plant associations: a *Spartina* zone on low ground and a *Salicornia* zone on the medium to high ground. The ground surface is extensively dissected by tidal sloughs or creeks. In the younger, *Spartina* zone the sloughs are fairly straight, running at nearly right angles to the bayfront; in the *Salicornia* zone the sloughs branch and wind tortuously (fig. 1). Eventually the sloughs, becoming narrower and shallower, lose their identity on the higher marsh. The highest marsh is covered by *Salicornia* and lies flat and unbroken by any waterway. Marshall (1948:211) called San Pablo marsh a "young marsh," meaning that it was primarily a *Spartina* marsh, actively being built onto the extensive bay mudflats. This is not entirely an adequate description, for in areas to the south of where Marshall worked most of the marsh is of the *Salicornia* type, and it is in this area that the present study was conducted.

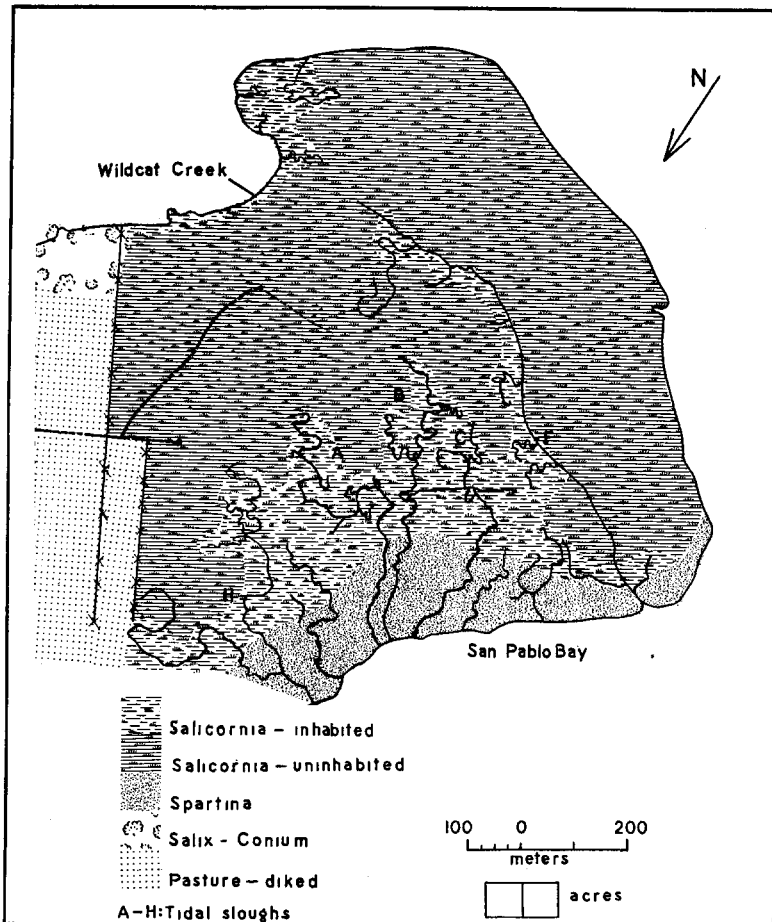


Fig. 1. Part of San Pablo salt marsh, showing vegetational associations and tidal sloughs on the study area.

The soil of the marsh is a heavy blue-black clay and on the lower marsh it is not built by deposition of plant material, but rather by the binding action of roots of *Spartina*. Anaerobic conditions exist in the soil of the *Spartina* zone a few millimeters from the surface and any disturbance of the surface demonstrates this by the immediate release of characteristic gasses, mainly H_2S , identifiable by odor. The soil is poorly drained and has a high water-holding capacity; if anywhere the surface is exposed to drying, marked shrinkage occurs with irregular surface peeling and polygonal cracking.

Vegetation.—The dominant plants of the *Spartina* association (fig. 2) are *Spartina foliosa* and, on the raised slough banks, *Salicornia ambigua*, *Grindelia cuneifolia*, and *Distichlis spicata*. The last three plants are properly classed with the *Salicornia* zone, and, indeed, penetrate the *Spartina* zone only on slough banks that effectively produce mid-marsh conditions because of their higher ground surface. *Spartina* generally is wetted by at least one tide each day. Where the marsh slopes gently into the bay and mudflat, there are found numerous young individuals of *Spartina* that extend the limit of the marsh.

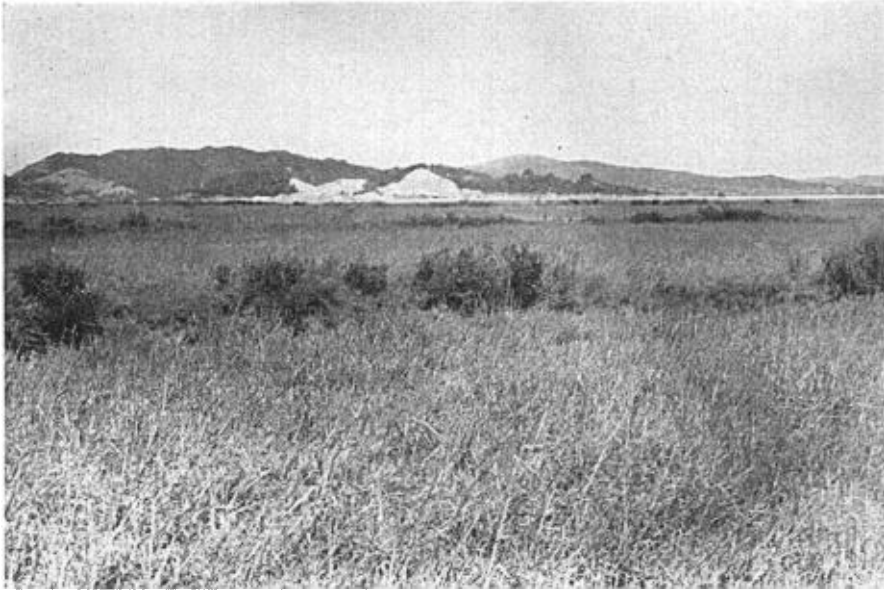


Fig. 2. *Spartina* association on San Pablo marsh. The shrubby plants are *Grindelia*, marking the banks of tidal sloughs.

Progressing to higher ground, tidal coverage, except in March and September when tides are very low, is reduced to only about one week per month in most months. Usually a band of variable width of *Distichlis* borders the *Spartina* zone, followed abruptly by the extensive *Salicornia* association (figs. 3 and 4). Plants of this zone in order of decreasing abundance are *Salicornia*, *Distichlis*, *Grindelia*, *Frankenia grandifolia*, *Jaumea carnosa*, *Triglochin striata*, *T. maritima*, *Cuscuta salina*, *Achillea millefolium*, *Cordylanthus maritima*, and *Atriplex patula*. *Spartina* enters this zone in the bottoms of the tidal sloughs and also occurs in depressions in the otherwise flat marsh surface. The distribution of the two vegetation types is indicated in figure 1.

Along their lengths the sloughs have undercut banks due to tidal flow and periodically parts of the banks fall into the water ways. This builds up the level of the slough bottoms and results in further deposition of soil both on the mudflats and on the highest marsh reached by the slough. In this manner the sloughs lose their identity on the high marsh, probably at about the same rate at which the marsh advances into the bay.

Tides.—Tides in this region of North America are of the semi-diurnal type, that is, there occur two high and two low tides practically every day of the year. Due to inequality between the lengths of the lunar and solar days the tides occur each day about one hour later than on the day preceding, and it happens occasionally that only three tides occur in a solar day. There is also an inequality in the range of the tides daily due to the variation in position of the moon north or south of the equator so that usually there is a higher high tide and a lower low, the other two tides being intermediate.

The heights reached by the tides vary throughout the year. This variation is due to the coincidence or opposition of solar and lunar attractions and the distance of the moon from the earth. Tides here are highest in the periods from December to January and June to July and lowest in March and September. This brief summary of tidal con-



Fig. 3. *Salicornia* association on San Pablo marsh. Foreground areas are not inhabited by Song Sparrows, which live in areas marked by the *Grindelia* rows in the middle distance.



Fig. 4. A tidal slough in the *Salicornia* zone; the slough here is 10 feet wide.

ditions in San Francisco Bay has been adapted from information in Miller, Ramage, and Lazier (1928).

The progression in range of the highest high tides in the spring of three years may be seen in figure 7. Here also is shown the fact that tides vary in their height one year to the next. With all heights referred to mean lower low water, the general range of the tides at San Pablo marsh is as follows (after U.S.C.G.S., 1949-1954):

Estimated highest tides ¹	7.5-9.0 ft.
Mean higher high water	5.8
Mean sea level	3.2
Mean lower low water	0.0
Lowest expected tide	-2.5

¹ Not from U.S.C.G.S. data.

The highest tide data have to be expressed as a range to account for the variation between years and to account for extreme climatic conditions. For example, it occasionally happens that the high tides in December are coupled with heavy rainfall and, infrequently, with winds that push surface water onto the marsh. The height of the tides is accordingly increased, probably from six inches to two feet, and especially so if the rains have been distributed over the entire central California basin, for then the Sacramento-San Joaquin drainage system adds a large amount of water to San Francisco Bay. The highest tide for any year will almost certainly occur in the winter even though June may have as high or higher readings in the tide tables.

The tides may be said to control the distribution of the plant species on the marsh, although other factors also operate. The lower limit to the range of any species seems to be closely related to the amount of submersion it can withstand (see Hinde, 1954), for, when plants are submerged, photosynthesis and gaseous exchange are greatly restricted. The interplay between the physiological characteristics of the plants, the elevation of the soil, and the height of the tides results in the zonation and interdigitation of the two plant associations on the marsh.

Interspecific relationships.—The relationships the Song Sparrow has with other animals and which were investigated in this study may be grouped into three categories: predatory, parasitic, and neutral or undetermined. The first of these is considered later, under "Mortality factors."

The Cowbird (*Molothrus ater*) is the only parasite on the Song Sparrow about which I have information. This parasite is of little consequence in the world of the salt-marsh Song Sparrow. This contrasts markedly with the situation found in Ohio and, presumably, in the eastern United States generally. Likewise it contrasts, but to a lesser degree, with the situation on Wildcat Creek, which flows down from the Berkeley Hills into San Pablo Bay.

On the marsh Cowbirds were seen in 1953, 1954, and 1955. In 1953 and 1955 the incidence was light and the birds seen were mostly single males. Females also occurred on the marsh, but my attention was not drawn to them. The incidence was heavier in 1954, at least one Cowbird being seen on most visits to the marsh from April through June. As many as six were seen one morning in May; this included two females. Notwithstanding this occurrence but two eggs and only one nestling of Cowbirds were seen on the marsh; presumably this means there was little reproduction by Cowbirds in the area.

The reasons for this lack seem obscure, unless they lie in the fact that Song Sparrow nests are difficult to find. Since Cowbirds are probably unfamiliar with the vegetation on salt marshes, they may have as much difficulty as do humans in finding nests of Song

Sparrows. They can with little difficulty find nests of Song Sparrows along Wildcat Creek; here Cowbirds are in familiar habitat and exist as a true breeding and fairly dense population.

The Red-bellied Harvest Mouse (*Reithrodontomys raviventris*) has a definite relationship with Song Sparrows. Probably only a part of it has been demonstrated by the present study. It is certain that adult harvest mice use old Song Sparrow nests for shelter and occasionally for their own nesting purposes. For the latter, the mice roof over a Song Sparrow nest and thus construct a fairly typical, spherical mouse nest. Litters of young mice have been found in such nests twice, and a total of five nests has been found in active use by harvest mice. All five sparrow nests used by the mice were of pairs of birds whose nesting attempts had failed early in the cycle, that is, eggs or very young nestlings had been removed by some agency and the nests deserted by the adult birds. The mice avoid nests that are flattened-out or encrusted with feces and excrement or littered with fragmented feather-sheaths.

Twice I have found adult mice using old Song Sparrow nests for shelter in daylight hours. These nests were not modified in any way; the mice were there on a temporary basis. What occurs when a mouse comes upon an actively used but momentarily unoccupied bird nest is not known. Such occurrences must be relatively common and it is probable that the birds drive off the mice. But when the attendant adult Song Sparrow is absent, the mice have a short period of time to themselves. The disappearance of single eggs and nestlings from nests may possibly be laid to the activities of the mice at this time.

The Savannah Sparrow (*Passerculus sandwichensis*) is an abundant permanent resident of the same marshes in which Song Sparrows live. Because Savannah Sparrows occupy the drier, grassier, upper marsh areas, there is only marginal contact between them and Song Sparrows. On the average about six pairs of Savannah Sparrows have nesting territories on the upper periphery of the area inhabited by Song Sparrows. Additionally, numerous Savannah Sparrows fairly regularly find foraging areas within Song Sparrow territories. But on only one occasion have I seen an act of aggression: a male Song Sparrow flew at a male Savannah Sparrow that was singing in the top of a *Grindelia* bush in the former's territory. Marshall (1948:204) concluded that, in spite of territorial overlap in edge situations, these two common species are not ecological competitors on salt marshes; my observations have repeatedly supported this.

ANNUAL CYCLE

Inception of breeding.—Factors influencing the time of inception of breeding in bird populations are known to be many. Most of them probably will be found to be closely correlated with the biological growing season in temperate regions. It has been demonstrated (Johnston, 1954:272) that there is a close relationship between the inception of the breeding season in several populations of Song Sparrows along the Pacific coast and the march of the biological growing season from south to north (the bioclimatic law of Hopkins). Populations of Song Sparrows are retarded in the inception of breeding by three to four days for each increasing degree of latitude.

Some of the factors that influence the timing of the biological growing season are thought to influence the inception of breeding by direct action on the bird. These are the photoperiod, the temperature of the two months before the breeding season, and probably also that of the preceding winter period (Davis and Davis, 1954:342), and the amount and temporal distribution of rainfall. Probably also very important is the effect of the three factors on the quality of food supporting Song Sparrows.

Other investigators have been able to show a correlation between inception of

breeding and some aspect of the temperature relationships beyond those involved in Hopkins' bioclimatic law. Thus, Nice spoke of a "temperature threshold" which, when reached, was followed by general breeding in the Song Sparrows she studied. Kluijver (1951:54) was able to show that Great Tits (*Parus major*) bred only after a certain amount of heat had been radiated to the surface of the earth; he summed the mean daily temperatures from the first of January to the date of inception of breeding in 16 successive years and found that the minimum "warmth-sum" was around 320°C. His data are very convincing.

I cannot show such correlations between salt-marsh Song Sparrows and their temperature environment. Table 1 shows the progression of temperature sums from Janu-

Table 1
Progressive Summation of Daily Mean Temperature in the Period January 1-March 25
at Richmond, California

	Day degrees in °Centigrade			
	1952	1953	1954	1955
Dec. 31	0	0	0	0
Jan. 15	110	185	152	110
Jan. 31	267	373	317	252
Feb. 15	443	559	475	415
Feb. 28	593 ²	704 ¹	640	551
Mar. 5	646	756	706	604
Mar. 10	696	830	768	672 ¹
Mar. 15	739	883	815	731
Mar. 20	783 ¹	937	863	798
Mar. 25	856	1010	917 ¹	872

¹ Date and temperature at which the earliest clutch was completed.

² February 29 is omitted from the summation; the mean temperature that day was 15.5°C.

ary 1 to March 25 for four years in intervals of 5 to 15 days. The temperature record was not made on San Pablo marsh but in Richmond, about one and one-half miles distant and at a height of 30 feet. All through the four years the summations are very close to one another. The sums have no direct relationship to the start of breeding, but it would appear that a minimum amount of heat necessary to produce conditions favorable to starting breeding is of the order of 650° to 700°C. But I do not want to say that any cause and effect relationship between a threshold or warmth-sum and inception of breeding exists in these birds. Temperature sums for this region for many years would show the same close agreement in summation. This is not a particularly noteworthy fact in itself, for central coastal California has essentially a maritime climate, one characteristic of which is a restricted seasonal and annual variation in temperature.

What importance to initiation of breeding the extremes and sudden shifts in temperature have is yet unexplored.

The influence of amount and distribution of rainfall on breeding is doubtless a complex one in temperate latitudes. It is worth mentioning that total winter-spring rainfall has no apparent relationship to the start of breeding in the present population. It is probable that the distribution of rain through the winter-spring season is as important as the total amount of rain that falls.

All these climatic phenomena influence the amount and nutritional quality of the spring vegetation, the invertebrate fauna of which is most important as food to Song Sparrows in the spring and summer. Factors in addition to the condition of the food

supply that influence the abundance and availability of invertebrates as food include winter temperature, success of the earliest yearly reproductive efforts, amount and distribution of rainfall, and, in the case of insects, the conditions at the time of flight. It is probable that the complex of factors subsumed by the term "food situation" is most important in regulating many aspects of the breeding cycle, including the timing of the start.

It should be emphasized that whatever factors are most instrumental in bringing about the onset of laying in this population they without much doubt act most tellingly on the female birds. As is mentioned later, males are sexually ready for breeding by at least mid-February but the bulk of the females are not ready for mating and laying until about four to six weeks later. Davis and Davis (1954:343) have noted the same thing in the English Sparrow (*Passer domesticus*); it occurs generally in passerine birds at mid-latitudes.

A special set of factors making for early breeding seem to be operative on salt-marsh Song Sparrows. These relate to the tidal fluctuation and are discussed on pp. 33-35.

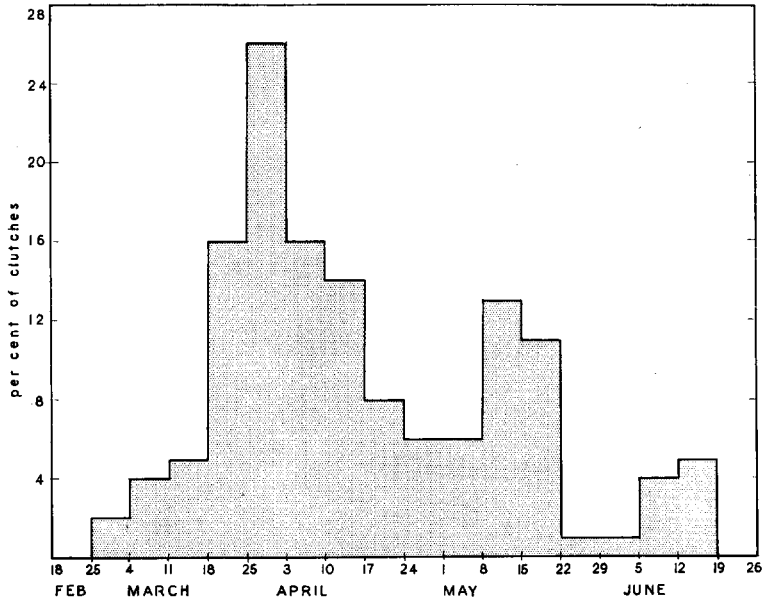


Fig. 5. Frequency distribution of completed clutches of salt-marsh Song Sparrows; $N = 111$ (1952-1954).

Breeding season.—The breeding season in *M. m. samuelis* is graphically illustrated in figure 5, which shows the span of the season and the frequency of nesting within that span. The birds breed generally from March to June, but they may occasionally go beyond these limits. Figure 5 indicates that there are three populationwide periods of general egg-laying: a main peak early in the season in which most of the birds on the marsh are active (late clutches of this group may actually be renestings), a second peak that involves renesting and second nestings, and a third peak that involves renesting efforts on the part of a relatively small part of the population.

This general picture masks the variation between years. The seasonal incidence of nesting for the same years as shown in figure 5 is graphed in figure 6. There were three nesting peaks in both 1953 and 1954; these followed regularly on one another at four-

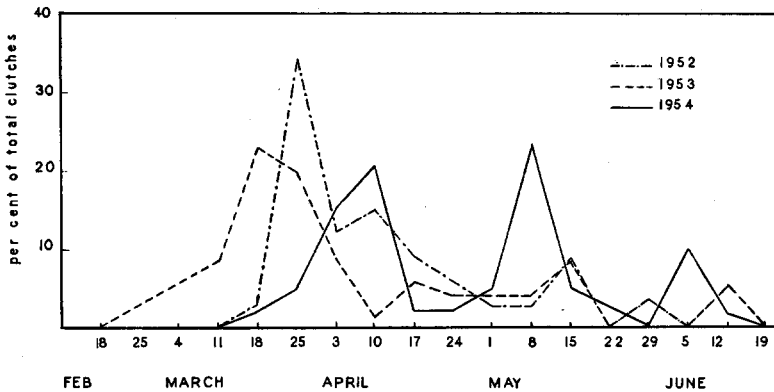


Fig. 6. Frequency distribution of completed clutches of salt-marsh Song Sparrows; 1952, $N = 31$; 1953, $N = 45$; 1954, $N = 35$.

week intervals. Since four weeks is not enough time to rear a brood of young Song Sparrows to independence, it is clear that relatively few successful breeders were involved in the activity represented by the peak following the time of their successful nesting. The four-week interval between successive completions of clutches indicates that these birds wait longer than a day before initiating reneating; Nice found that Ohio Song Sparrows had a new nest with an egg only five days after the destruction of a previous nest, and it takes four days to build a nest.

Table 2

Schedule of Events During the Early Breeding Season in Two Populations of Song Sparrows Around San Francisco Bay¹

Population	Inception of breeding		Peak of breeding
	Earliest date	Mean date	Modal date of first clutches
San Pablo salt marsh	Feb. 28	Mar. 16	Mar. 28
North-bay uplands	Mar. 25	Apr. 1	Apr. 15

¹ Data from Johnston (1954:272).

It has been noted previously that salt-marsh Song Sparrows breed earlier than upland Song Sparrows at identical latitudes (Johnston, 1954:270); the time involved is of the order of fifteen days (table 2). It seems likely that this early nesting represents an adaptation on the part of the marsh birds to the conditions of tidal flux and wane, since the first and major nesting effort of the population occurs during the time of minimum tidal heights for the whole spring season (fig. 7, data from U.S.C.G.S., 1951-1954). As the graphs of the tidal progression indicate, the maximum heights of the high-high tides in the three years varied strikingly. Nevertheless, the maximum height of the tides bore only a general relation to the mortality caused to young Song Sparrows in any year.

The year 1954 had the highest high tides of the period from 1952 to 1954 and also the highest actual egg-nestling mortality of the three years. But the lower tides of 1952 caused a greater per cent mortality than the higher tides in 1953. The difference is not statistically significant, but it does not invalidate the point that the height of the tide may not stand in direct relationship to the number of young Song Sparrows killed. The

most important factor reducing egg and nestling mortality in 1953 seems to be the fact that the population undertook very early general breeding; over 60 per cent of the eggs laid that season had already fledged young before the first serious high tide came over the marsh. The hypothesis is that selection has fitted the Song Sparrows of the marsh to early breeding so that, given a normal set of environmental circumstances, the birds breed before the high run of high tides and thus escape a chief cause of mortality in the young age classes.

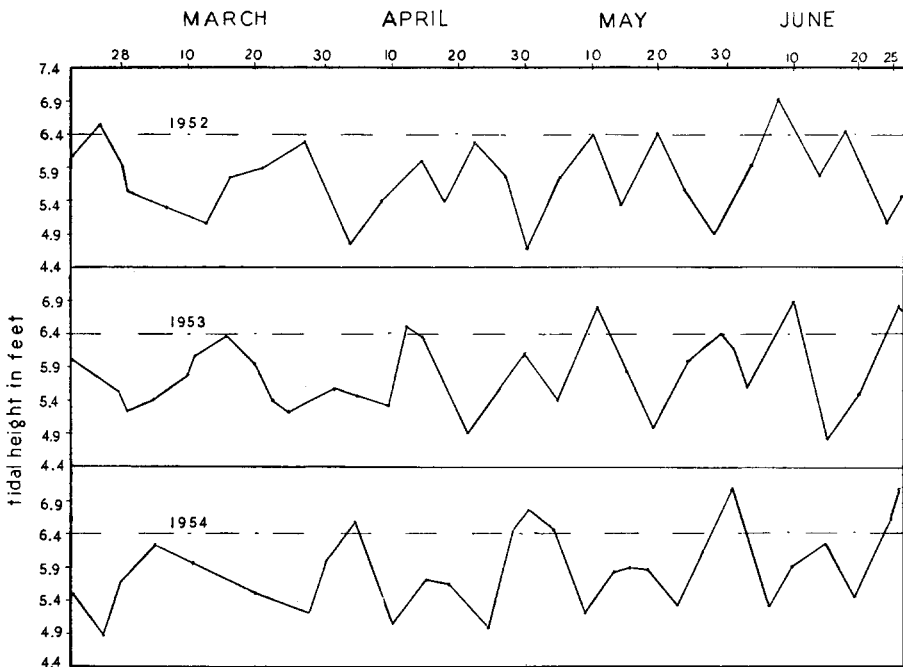


Fig. 7. Variation in the heights of the highest spring tides on San Pablo marsh, 1952-1954.

Most tides that reach 6.4 feet or higher on the marsh are high enough to flood nests of Song Sparrows. Table 3 shows the relationship between tides reaching at least 6.4 feet in three different breeding seasons and the number of deaths caused to Song Sparrows as a direct result of the high tidewater. In the three years the number of days having the high tides varied between 14 and 20 per cent of the total number of days that

Table 3

The Relationship between High Tides and Mortality of Young Song Sparrows on San Pablo Marsh

Year	Length of season in days	Days tide reached 6.4 feet or higher		Mortality of young birds		
		Number	Per cent of season	Number of eggs per season	Young killed Number	Per cent
1952	104	15	14.4	107	8	8.5
1953	125	24	19.1	140	4	2.8
1954	99	20	20.2	102	19	18.2

the population of Song Sparrows was engaged in breeding. At the same time the mortality caused to eggs and nestlings varied from a negligible fraction to almost one-fifth of the total number of eggs laid for the year. There is no correlation between the number of high tides and the amount of mortality to young birds caused by them, according to these data.

With respect to the tides, the pattern of normal nesting activity is as follows: When the tidal cycle is on a downswing, through February, Song Sparrows approach breeding, and males are ready to breed by mid-February; laying usually begins some time in March. The bulk of the population has usually completed clutches by the last week in March and the young of these first nestings leave the nest before the fairly high tides of late April. There follows an upswing of nesting activity in May, the resultant young leaving the nests before the high tides of early June occur. Subsequent to this only sporadic nesting is found in the population and much of this is flooded by the very high tides later in June.

Any low-positioned nest on the marsh stands in danger of being flooded even by such relatively low high tides as those reaching 6.2 feet. Eggs are floated away and nestlings under the age of eight days are drowned; a nestling eight days old is capable of climbing up in the vegetation above the nest and many escape drowning in this manner. Therefore, since June and July have frequent high tides, late nesting probably has no selective advantage in this population, and may actually work to its disadvantage, for nesting activities are physically taxing, and conspicuous, territorial males are more subject to predation. But, early nesting may be considered to be advantageous, for the reasons already outlined.

When the typical early nesting season is delayed, it is abundantly clear that the salt-marsh Song Sparrows suffer drastic consequences. The season of 1954 saw retarded breeding both in salt-marsh and upland Song Sparrows, and by the time nestlings of the marsh birds were in the nest the high tides of late April and early May inundated the marsh; all nestlings under eight days of age were drowned. Of a total of 17 nestlings of all ages under observation at this time, 12 were killed and 5 saved themselves by climbing above the water level. The same thing on a reduced scale occurred in both the second and third nestings and the total seasonal productivity was near the lowest recorded for the population.

The productivity was in fact so low that it did not suffice to maintain the population at the level at which it had been for the two years preceding, and the density in 1955 was 14 per cent below that of 1954. The data on density and productivity will be presented later.

Nests are placed off the ground in all cases, most commonly in *Salicornia*, *Grindelia*, *Distichlis*, and *Spartina*. Since the average height of this vegetation is less than two feet, nowhere can the birds nest in high places. Yet nests placed lower than five inches above the ground surface are flooded. It is not by chance then that nests average about nine and one-half inches high over the whole marsh and about twelve inches on the lower marsh. Nests are most frequently placed as high in a particular site as they can be and still be afforded the vegetational cover that is apparently necessary for the nest contents and the adult occupant. However, the birds do not often choose for the nest site the tallest vegetation available to them in a given territory; predators, mostly mammalian, probably also exert a selective pressure to the end that Song Sparrows use those sites suited to meeting the whole environment. Nests are never used twice and the several nests of any one season are placed in different parts of the territories.

Generally, with the increase in the height of the vegetation as the breeding season progresses, it is possible for the birds to nest at successively higher levels. This parallels

also the increase in tidal heights through the season. Data are sparse on this point, but in June no nest lower than ten inches off the ground has been found.

It is difficult to estimate accurately the number of times a pair of salt-marsh Song Sparrows nests in one breeding season. It is more difficult to find every nest of ten or twenty breeding pairs in one season and thus speak of averages. I know with certainty that practically every pair will nest twice in any season. The data of Nice (1937:134) show that for the year 1930 twelve of the pairs she watched in Ohio nested three times in the season and four pairs nested four times. The average number of nestings per pair was 3.25 per season.

I include these figures to indicate the general expectancy of number of nestings per season. Since nests of salt-marsh Song Sparrows are difficult to find and since observations indicate many nestings for which I have no record, I have assumed that each pair of birds had one more nest that I was unable to detect. Moreover, if a pair was observed to have two nests before half the breeding season was over, I have credited them with an additional nesting effort. Averages calculated on these bases are 2.5 nestings per pair in 1952, 1954, and 1955 and 3.0 nestings in 1953. These guesses do not seem high if it is considered that all nesting attempts are included, not just the successful ones.

Clutch-size.—Clutch-size is another characteristic that has been found to vary between populations of Song Sparrows. The birds of San Pablo marsh have a lower clutch-size than that found in any other population of Song Sparrows at comparable latitudes across the United States. The only population that resembles *samuelis* is that found on the lower reaches of San Francisco Bay, namely *pusillula* (Johnston, 1954:272); since this group too lives in a salt-marsh environment, it appears that the factors operating to control the size of clutches are the same in the two marsh areas. Further, the physiologic response on the part of the two races of birds must also be similar.

Lack (1946, 1947*a*, 1947*b*) has already given an indication of the variation in clutch-size to be found inter-seasonally and intra-seasonally, between birds-of-the-year and adults, and geographically for many species of birds, and Kluijver has catalogued similar variations for local populations of the Great Tit.

Table 4

Variation in Clutch-size in Song Sparrows on San Pablo Marsh

Breeding season	Time of year						Seasonal mean $\pm \theta$	S. D.
	Feb. 28–Apr. 5		Apr. 6–May 25		May 26–July 1			
	Number of nests	Mean clutch	Number of nests	Mean clutch	Number of nests	Mean clutch		
1950–51	9	3.22	6	3.66	1	3	3.37 \pm 0.12	0.48
1952	14	3.35	16	3.56	1	3	3.42 \pm 0.10	0.57
1953	27	2.92	14	3.29	4	3.25	3.04 \pm 0.09	0.61
1954	6	2.83	24	3.00	5	2.60	2.91 \pm 0.09	0.56
1955	9	3.11	17	3.23	4	3.50	3.23 \pm 0.09	0.50
1950–55	65	3.08	77	3.23	15	3.07	3.20 \pm 0.05	0.60

It is apparent from the data in table 4 that average clutch-size is occasionally an oversimplification, for it masks important seasonal and yearly shifts in clutch-size. There is first the typical seasonal progression in clutch-size from a low value early in the season to a high in mid-season, dropping again lower at the end of the season; this pattern has been noted in a variety of passerine birds and is linked presumably to the food situation (Lack, 1947*a*). Secondly, there is evident a yearly shift in the size of clutches.

Annual variation such as this has many controls; known and hypothetical controls for salt-marsh Song Sparrows are diagrammed in figure 8.

I believe Lack is right in postulating that the size of the clutch with regard to yearly variation is a reflection of the number of young that the adults can successfully rear at one time; certainly the data on brood size and nestling survival in the Common Swift (*Apus apus*) strongly support the thesis (Lack and Lack, 1951:517). The proximate factor controlling clutch-size can now only be guessed at, in the absence of critical physiological data, but the major environmental variant that impinges on a pair of birds in nesting and rearing a brood of young is the availability and quality of food.

Even though this may almost be taken as a truism, little direct evidence can be found to support it. Lehmann (1953:225) has shown the seasonal decrease in clutch-size in the Bobwhite (*Colinus virginianus*) is paralleled by the amount of decrease of stored vitamin A in the liver. This is all the more suggestive when it is considered that he also found that a reduction in the amount of vitamin A in the diet of the Bobwhite retards the inception of breeding and may even prevent some individuals in a population from breeding at all in a given year. This happens in years that have low spring rainfall with a subsequent stunting of green vegetation, which is the birds' main source of vitamin A prior to breeding.

These correlations merit serious consideration in any theory on the control of annual variation in clutch-size, although more evidence obviously is needed for any one species; certainly other aspects of the qualitative nature of food may be also operative.

The low clutch-size (table 4) recorded for Song Sparrows in mid-season of 1953 should be mentioned here. At the time that the birds were initiating these clutches, for second and re-nestings, there was already a major increase in population number due to the production of young from the earlier and numerous first nestings. Possibly this increase in the number of Song Sparrows on the marsh left the increased food supply expected at that time again in relatively short supply. It is perhaps in this way that population density influences clutch-size: there is an interplay between a fluctuating food supply and a fluctuating abundance of birds, in which the absolute number of items in either category is less important than the balance obtaining between them.

Figure 8 diagrams the possible relationships between the several factors that may influence annual and seasonal variation in clutch-size in salt-marsh Song Sparrows. The relationships, although possibly obvious, are also sufficiently complex as to deny simple analyses. As a general rule in nature, a reduced mortality rate does not in itself mean a species or population will have a higher density of population. Yet in salt-marsh Song Sparrows, one year's density depends largely on the preceding year's production of fledglings; this in turn is largely influenced by mortality of young in the nests. Evidence for this will be presented in Part II.

A high population density seems certain to work to reduce the relative amount of food available to any given female bird, probably through constriction of the size of the territory; in these birds the size of the territory varies with density. Variations in density may also make themselves felt in other, as yet unknown, ways; I have grouped these hypothetical effects in the box labeled "psychological state."

The physiological effects, along with the psychological effects, are catch-all categories, reflecting ignorance concerning proximate determinants of clutch-size. So, to a lesser degree, is the term "individual genetic limits" a reflection of our ignorance. But it may be assumed that such things as the average annual mortality rate, the general food situation with respect to the number of young that may be fed, and the number of eggs that can be covered by the sitting bird have a causal relationship in the determination of genetic limits of clutch-size for a species.

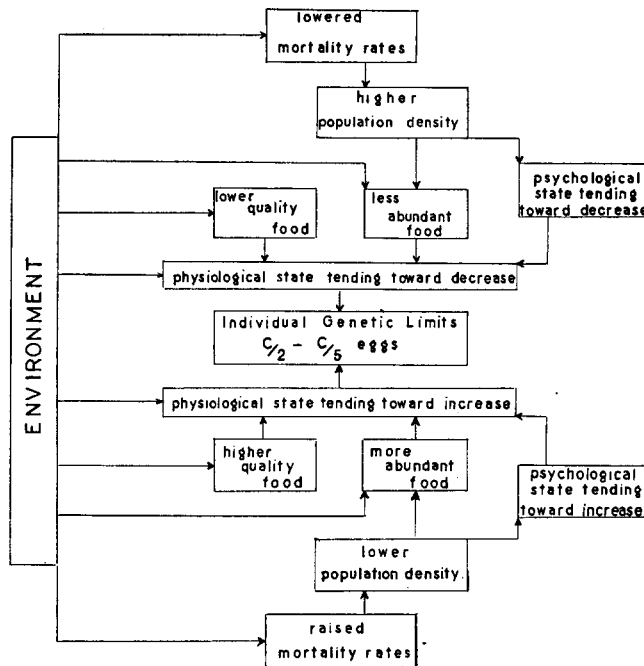


Fig. 8. Factors influencing annual and seasonal variation in clutch-size of salt-marsh Song Sparrows.

Territory and movement of adults.—Territorial relationships of Song Sparrows on San Pablo marsh are typical of those of the species elsewhere. There is only a slightly earlier inception of most features of the annual cycle. In late winter and spring there is evident a rise in the incidence of songs of males and of other aggressive habit patterns, such as pursuits. By late February and early March territories are set out by almost all males on the marsh. There are usually a few trios yet to be found in areas that normally would comprise a territory at this time, but these situations are resolved at the latest by the first of April.

Singing decreases during the latter half of March and in April. Territorial strife as manifested by chases and periodic singing is to be noted during the whole of the breeding season, but these occurrences are momentary and are not a large part of Song Sparrow activity at this time. Following breeding and beginning with the inception of molt in early July there is an almost complete cessation of territorial activity. It is during this period of territorial inactivity and that time immediately preceding it that juvenal Song Sparrows disperse through the population; it should be noted that juvenal birds are tolerated in breeding territories in April and May; aggression is restricted to adult birds.

In late August and into September, when molt is almost completed, there is a noticeable rise in territorial activity. Both birds-of-the-year and adults become more aggressive. One result of this, apparently, is to bring to a halt further dispersal of young birds. But, true territories are not staked out, for in some cases three to six birds are found in an area normally comprising one breeding territory. These groups possibly are comparable to the groups Nice (1937:63) recorded in winter; it is certain that they are not

family groups. However, in the majority of cases two birds, a pair, will be found in each such area.

By the time of breeding in the following year, occupants of territories are reduced to a complement of two, or, rarely, three birds. The extra birds are, without much question, young-of-the-year; probably also they are males. In all instances two of the three birds contended for territorial possession and the third individual qualified merely as an interested onlooker. The latest date on which any trios have been seen has been during the first week of concerted breeding activity in any year; a specific date is March 26, 1954. I do not know what happens to the extra birds except that eventually they disappear from the territories. It seems likely that some fall to predators or move only slightly to a neighboring area if the opportunity presents itself. It is certain that the birds do not move far if only one banded bird has been found to move under such circumstances.

Indications from previous studies are that Song Sparrows are highly sedentary with respect to the breeding territory (Nice, 1937; Miller, 1947). Salt-marsh Song Sparrows have an extremely strong attachment to the breeding territory; this is evident throughout the year. The birds are found in the area of the breeding territory (the "domicile" of Kluijver, 1951:22) even when territory is not actively being defended. Doubtless this high degree of "ortstreue" is related in some way to the essentially non-migratory habit of these birds. It would appear to be easier for a bird to remain in its territory of the previous year if it ventured away no more than 100 or 200 yards, than if it undertook migration.

The closest approximation to migratory movements shown by Song Sparrows of San Pablo marsh occurred in a small area of tall *Salicornia* on the high marsh, where, in 1952 and 1953, the birds bred. In the summer of those years the birds moved out and returned only in winter when the area became moist enough due to the winter rains. In the dry years of 1954 and 1955 there was no occupation of or breeding in this area. I consider this to be an irregular occupation of a marginal habitat rather than true migration. I have included none of the individual birds that moved this way in the data in table 5 on movement of adults, for movement on the lower marsh, where habitat changes are minor through the year, if of a different nature.

Table 5

Changes in Position of Territory of Adult Salt Marsh Song Sparrows from One Breeding Season to the Next

Distance moved ¹	Males	Females	Total ²
0-15	27	16	43
16-25	1	2	3
26-35	1	1	2

¹Center to center of territory.

²Forty-eight cases but 24 birds; see text.

Table 5 shows the distance between centers of breeding territories in successive years for 24 Song Sparrows. Individual birds appear in the table one or more times, depending on the number of years they held territory according to my records. The 24 individuals furnish 48 records of possible movement from one year's territory to the next. Roughly one-ninth of the sample is seen to have undertaken movement of a relatively short distance. This is a significant part of the whole, but the importance of this to the structure of the population is reduced by the fact that the movement is on such a minor scale. von Haartman (1949:62) used 0.10 kilometer as his smallest unit in dis-

curring movement of adult birds of several species; this unit is too large for analysis of the present data. Basically the important fact obtained from the data is that the movement is almost wholly of a scale less than the dimensions of a territory; eight birds that moved averaged 16 meters each.

Dispersal of juveniles.—The major means by which transfers of individuals occurs between populations of non-migratory Song Sparrows is dispersal of young birds. This probably also is true for most species of non-migratory birds, for young birds are not attached to their places of origin as are adults to their breeding territories. Dispersal, or movement by young from their places of birth to their places of eventual breeding, is an important adaptation for all sedentary species of animals, if not for more mobile ones, for its existence ensures a tendency in time toward a greater degree of panmixia than otherwise would be possible; there is, in Miller's (1947) expression, a graded panmixia in space and time.

This means that a large population consists of relatively small completely interbreeding subunits in any given breeding season. According to present theory (Wright, 1932:361; 1950:247) this is a favorable situation for maintaining a genetically healthy population, since none of the subunits exists genetically isolated in time long enough to allow fixation by chance of deleterious alleles, yet varieties of genetic combinations are given opportunity, so to speak, to demonstrate survival value.

In salt-marsh Song Sparrows dispersal by the young takes place in the summer of the year, or when the birds are at least one month old but probably before they are two months old. Individuals disperse independently of one another; Goodbody (1952:285) and Gibb (1954:44) noted an "explosive" or sudden dispersal in banded titmice (*Parus*) when they reached three or four weeks in age. After August and September no additional effective movement occurs among Song Sparrows. That this apparent attachment to what amounts to the future breeding territory takes place in a bird's third or fourth month of life is not surprising, for in August each year there is a marked upswing in territoriality; this would tend to inhibit further, indiscriminate wandering through the marsh. In titmice neither Goodbody (*loc. cit.*) or Kluijver (1951:30) noted such a cessation of movement; dispersal with these species continued to February or March.

In graphing the records of dispersal (fig. 9) I have included data obtained from individual banded Song Sparrows observed from August through to the following breeding season, regardless of the fact that some of the individuals seen before the time of initiation of strict territoriality in the spring did not live to breed. Nineteen of the 34 records are for such birds. A comparison of the territorial and non-territorial groups shows that there is no difference between them in the median distance of dispersal, but a slight although statistically insignificant difference in the less meaningful average distance of dispersal. One bird did move from the area it had ostensibly dispersed to in September; in the following March the bird was found 150 meters distant. The "original" distance of dispersal was 185 meters, the final 300 meters.

In converting the field observations to quantitative data I measured with fine-pointed dividers the shortest straight-line distance between the two areas involved in dispersal for any one individual on the United States Production and Marketing Administration aerial photograph number BUU-9G-57, which covers San Pablo marsh. This measure was converted to linear distance.

The absence in this sample of juvenal birds moving 500 to 600 meters deserves special comment. In the first instance, there are proportionally fewer spots on the marsh 500 to 600 meters from nest sites, which also are habitable by Song Sparrows, than there are those that occur less than 500 and more than 600 meters. This is due to the vast expanses of low *Salicornia* on the upper marsh. Secondly, there is apparently a tendency

for the birds to follow the courses of the tidal sloughs, along which their preferred cover grows; there is less of a tendency for the birds to leave the sloughs and cross open ground, but this occasionally they do. Another possible reason for this gap in the records of dispersal is that juvenal birds may be differentially endowed with an instinct to disperse. This suggestive line is pursued beyond.

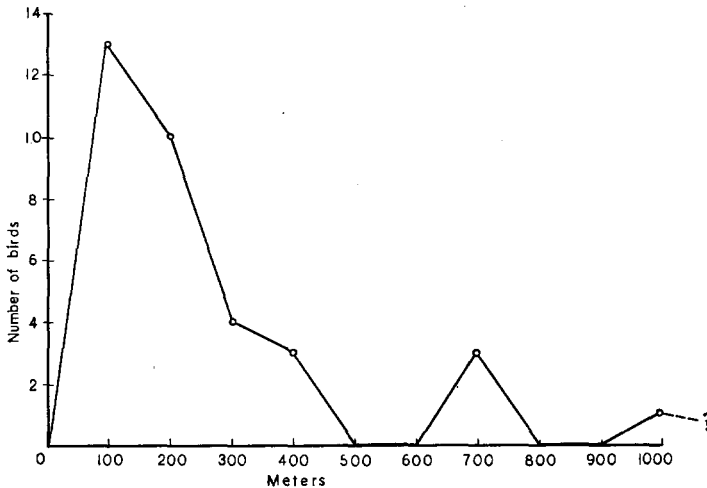


Fig. 9. Distance of dispersal of juvenal salt-marsh Song Sparrows, hatching site to breeding site.

The data shown in figure 9 represent dispersal of the most limited degree yet found in any bird population. The median distance of dispersal is 185 meters, about 100 meters less than that found for Ohio Song Sparrows (Miller, 1947:188). The extreme distances recorded for the salt-marsh birds are 30 and 960 meters. Forty-two per cent of the juveniles settled within 150 meters of their point of origin, 66 per cent within 250 meters, and 81 per cent within 360 meters.

One other example that approaches this pattern of dispersal is that found in European populations of the Starling (*Sturnus vulgaris*) as detailed by Kluijver (1935), but the median distance of dispersal for this population was close to 400 meters, and the mean over 500 meters. Farner (1945:91), von Haartman (1949:63), Kluijver (1951:14), Kendeigh (1941:18), Lack (1953:116), and Ruiter (1941) all dealt with species that showed dispersal to great distances.

It remains yet to examine the dispersal to see whether these results are a function of directed movement or if they may have occurred at random. The random occurrence of isolated events in a continuum is effectively described mathematically by the Poisson distribution; if the distribution of these salt-marsh Song Sparrows parallels that calculated by the Poisson distribution, then it may be assumed that this dispersal is random and undirected.

I have calculated Poisson distributions using the present data and Mrs. Nice's data for the Ohio Song Sparrows and have compared them with the observed cases of dispersal in both populations (table 6). The Ohio population has been included here for comparison with the salt-marsh population, for the similarities are striking and suggestive of a common pattern. Both groups of Song Sparrows are found to have curves describing their dispersal that differ from expectation significantly at the one per cent

Table 6
Observed and Computed Distribution of Dispersal in Two Populations of Song Sparrows

	Distance of dispersal in meters							
	100	200	300	400	500	600	700	800+
California								
Per cent expected	30.6	25.6	20.7	12.4	5.9	2.3	0.7	1.8
Per cent observed	39	30	12	8	0	0	8	3+
Ohio								
Per cent expected	22.8	23.5	22.8	15.5	8.6	3.3	1.0	2.5
Per cent observed	12	27	30	8	6	8	3	6

level. For the California sample, the main characteristics of the observed curve of dispersal that deny a random nature are that fewer birds move to intermediate distances (350 to 650 meters) and more birds move to distances beyond 650 meters than the Poisson distribution requires. There is also a tendency for the birds to aggregate more than expected at the lower end of the curve, but it is possible that the results listed here could have occurred by chance, as chi-square gives significance only at the ten per cent level.

It is to be noted that about ten per cent of the Song Sparrows in both the California and Ohio samples moved to the greater distances; possibly this mirrors a definite drive in this small part of the whole to move great distances. On this basis it would have to be assumed that the bulk of the dispersing juveniles have no strong drive to move anywhere. This is not inconsistent with the fact that no other bird species has so restricted a dispersal; the young of such species as *Troglodytes aëdon* (Kendeigh, *op. cit.*), *Phoenicurus phoenicurus* (Ruiter, *op. cit.*), *Muscicapa hypoleuca* (von Haartman, 1949:60), and probably also *Saxicola rubetra* (Schmidt and Hantge, 1954) have very little tendency to aggregate, dispersing uniformly to great distances through suitable habitat. The proposed existence of a small fraction of the juveniles that are hereditarily endowed with a tendency to disperse to great distances merits comment. The fact that both the salt-marsh and Ohio Song Sparrows show a group of juveniles that move great distances suggests that this is a real phenomenon. Reasons for this peculiarly endowed fraction of the population may be found in the selective advantages of gene interchange between semi-isolated populations, as expanded by Wright. Noteworthy also is the hypothesis of a similar basis for long-distance dispersal in *Peromyscus* by Dice and Howard (1951).

SUMMARY

A population study of Song Sparrows of the race *Melospiza melodia samuelis* was carried out in the years 1950-1955 on San Pablo salt marsh, Contra Costa County, California, by means of color-banding; 287 individuals were banded.

San Pablo marsh is a typical San Francisco Bay salt marsh, grown to a *Spartina* association on lower levels and a *Salicornia* association on higher ground. The tidal range is -2.5 to 9.0 feet; mean higher high water is 5.8 feet.

Factors influencing the initiation of breeding in the Song Sparrow are closely associated with the biological growing season and include the photoperiod, temperature of the preceding three months, and the amount and distribution of the winter rainfall; these influence also the amount and quality of the Song Sparrow's food, which may well be the most proximate factor. The inception of breeding seems not to be closely related to any "temperature threshold" or "warmth-sum."

Breeding spans the period from March to June; the peak of first nestings is March 28. This is more than two weeks earlier than in upland Song Sparrows at the same latitude; this seems to represent an adaptation to marsh life, for the birds thus nest mainly

during lower tidal conditions. It is shown that it is not the absolute height of the tides that governs egg and nestling mortality, but whether or not the birds can nest early enough to escape the high run of tides in April to June; when they breed late, there is high mortality caused by the high tides.

Clutch-size in this population averages 3.20 eggs, but may be as low as 2.91 (1954) or as high as 3.42 (1952). Environmental variations that induce variation within the genetically determined limits of clutch-size are thought to include quality and quantity of food, population density, and mortality rates.

Male Song Sparrows set up territory through the late fall and winter and are completely territorial by late February. Territorial defense is lacking from July to September when the adults molt; autumnal territoriality is seen in mid-September. Adult birds rarely shift territory from one breeding season to the next, and of eight that did the average distance, center to center of territory, was 16 meters. Dispersal of juveniles occurs in the late spring and summer and halts in late August and September when territorial activity rises. The median distance of dispersal, hatch-site to breeding-site, for 34 Song Sparrows was 185 meters. The limited adult movement and restricted distance of dispersal of these Song Sparrows mark them as the most sedentary population of birds yet investigated. Nearly 10 per cent of the juveniles seem to have a tendency toward dispersal to relatively great distance.

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