POPULATION STRUCTURE IN SALT MARSH SONG SPARROWS
PART II: DENSITY, AGE STRUCTURE, AND MAINTENANCE

By RICHARD F. JOHNSTON

This is the second part of a report on the population ecology of the Song Sparrows (*Melospiza melodia*) living on the salt marshes of the north part of San Francisco Bay. Part I (Johnston, 1956) dealt with a description of the environment of salt marsh Song Sparrows and with their breeding behavior and movements. This part treats demographic considerations.

POPULATION DENSITY

There are several ways to describe the relationships between numbers of Song Sparrows and the area in which they live. The figure of 105 pairs of Song Sparrows per 100 acres given earlier (Johnston, 1952:316) for the population here discussed does not indicate the true density this species maintains, for the areal reference in this measurement was for a total study plot, 80 to 90 per cent of which Song Sparrows do not inhabit. However, this density figure is comparable to certain figures recorded by workers in population ecology and thus has relative meaning.

As described previously, salt marsh Song Sparrows live along tidal sloughs and except in places where the sloughs double back on themselves the territories of the birds are strung out one by one along the lengths of the sloughs. The birds thus occupy effectively only a fragment of the total marsh (fig. 1). Sporadic foraging or trips to gather nesting material occur in the regions between the sloughs, and dispersing juveniles must also cross these areas, but in a practical sense these areas of short *Salicornia* are not used by the birds. If a marsh is totally grown to short *Salicornia*, the Song Sparrows are not resident there (Marshall, 1948*a*:214).

Table 1 shows the relationships between numbers of birds and the lengths and areas of four major sloughs on San Pablo marsh in the breeding season of 1953, a year of high density. The areal calculation for each slough was made by multiplying the length of the slough by 30 feet. Thirty feet represents the average width of territories along sloughs within which the birds perform practically all their activities. At high water a 6- to 10-foot strip of water is present, but at lower levels a great deal of mudbank is exposed; this last is, of course, ideal Song Sparrow foraging area. With this as the definition of the area in which Song Sparrows live, the actual density in a year of high numbers is seen to run from 8 to 10 pairs per acre. This is not as unreasonable as it may seem, for 10 pairs of Song Sparrows per acre would give each pair about 4350 square feet per territory; this amounts to a rectangular plot about 30 by 150 feet on the sides. This is the size of many territories on the marsh, although some are smaller and some larger.

Figure 1 outlines the changes in territorial utilization of the area along one of the major sloughs ("A") on the marsh for five successive breeding seasons. This can be taken as exemplary of the similar shifts in placement and number that occurred in other parts of the marsh. The shifts themselves are of interest, but perhaps the most significant thing illustrated in the figure is that there is a clear difference in size of breeding territories in relation to the vegetational configuration of the immediate area.

In the *Spartina* zone territories are larger than those in the *Salicornia* zone. However, at the heads of the sloughs the height and amount of vegetation, especially that of *Grindelia,* is reduced, and territories here are larger than those in the mid-marsh areas of lusher vegetation. For these reasons the two longer sloughs listed in table 1 have a lower density than the shorter sloughs. Both B and H have long stretches in the *Spartina* zone and both have at least two arms leading to the less complex vegetation of the upper portions of the sloughs.

In the six-year period from 1950 to 1955 the number of Song Sparrows on the marsh plot remained relatively constant. Table 2 lists the changes in breeding density observed for this period of time. The largest change was a 24 per cent increase for 1953 over 1952. All other changes of density are of a low order of magnitude. Figures for the years 1950 and 1951 are extrapolations from counts for smaller areas, as accurate counts were made of only a portion of the plot used in later years.

Table 1

Linear and Actual Density of Song Sparrows on San Pablo Marsh in 1953

Slough	Length (feet)	Acres[1]	Pairs of Song Sparrows	Density Linear[2]	Density Actual[3]
A	3060	2.1	22	139	10.5
B	3575	2.5	24	153	9.7
C	2400	1.6	17	130	10.4
H	4480	3.0	25	170	8.2

---

[1] Length of slough ×30 feet. [2] Number of feet per pair. [3] Number of pairs per acre.

The greatest change in density recorded in table 2, that in 1953, was not, by ordinary populational standards, a large increase; likewise none of the decreases were large. It may thus be assumed that this population exists in fair equilibrium with its environment. Nonetheless, the fluctuations in density were not random in character. The changes can be related to the productivity of the previous year (fig. 2).

Table 2

Changes in Density of Song Sparrows on 100 Acres of Salt Marsh

Year	Pairs of breeding adults	Change in density in per cent of previous year
1950	87[1]	....
1951	90[1]	3
1952	100	10
1953	124	24
1954	118	5
1955	102	14

---

[1] Estimates based on counts of smaller areas.

Figure 2 plots both productivity and population density against time. The ordinate on the left represents population density in the several years as percentages of the density recorded for 1952; the ordinate on the right, an entirely different scale, represents yearly productivity in absolute numbers. The two curves allow direct comparison between productivity for a given year and the subsequent year's population density. It is apparent that high productivity can be correlated with a succeeding rise in population density, for in every case an increase or decrease in density is preceded by an increase or decrease in the productivity of the year before. Whereas this apparently causal relationship is not surprising, it has not heretofore been demonstrated among passerine birds and Gibb (1954:42) has shown that it does not hold for Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*) in the English midlands.

There is no demonstrable reverse relationship among salt marsh Song Sparrows; that is, density does not seem to influence the same year's productivity. Many previous

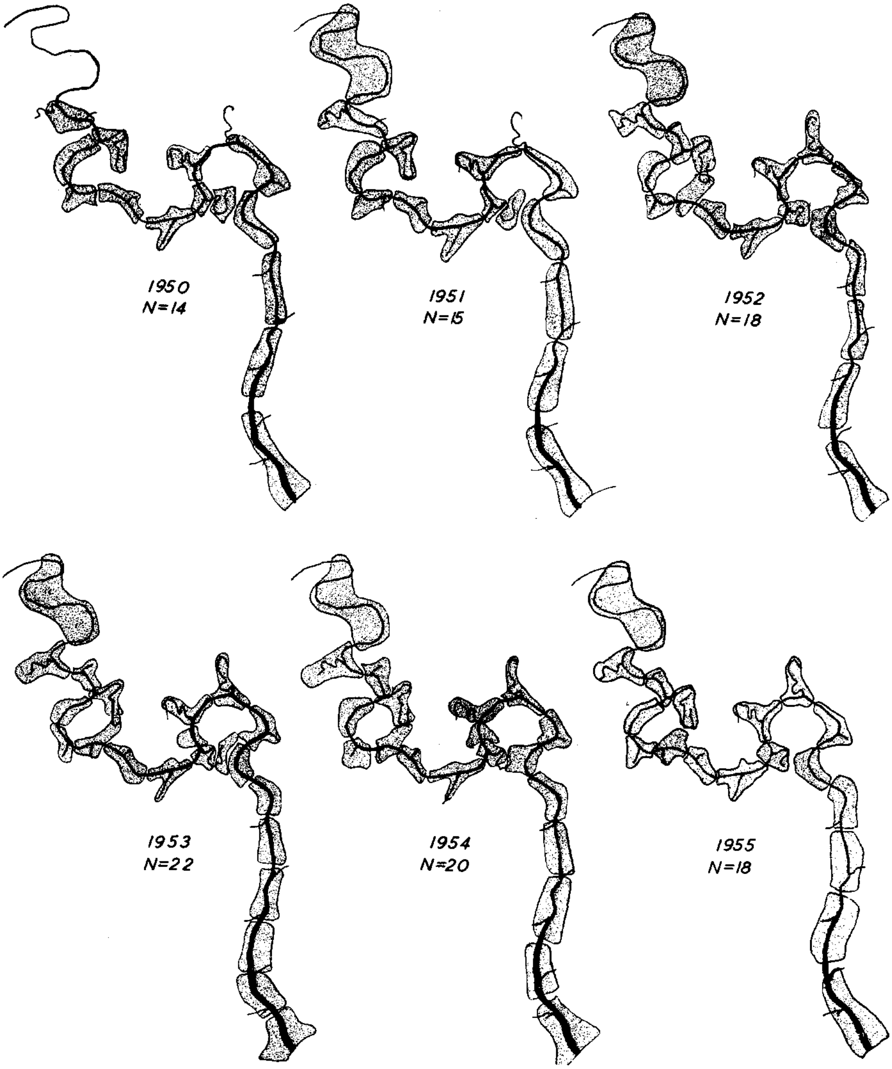

Fig. 1. Breeding territories of salt marsh Song Sparrows along one tidal slough ("A").

workers have made an effort to show that density is its own automatic control, and the argument now is strong that extremely high densities by their very nature react upon themselves so as to cause or guide a reduction in density. But, most populations of vertebrate animals in temperate regions never reach extreme densities. Thus, in these Song Sparrows the relatively small variation in density from year to year appears not to influence a subsequent year's density. The influence of such things as the number and size of useable territories is probably stringent enough that the maximum density is never "high," any excess of individuals spilling out into marginal areas, and the habitat is not strained as a result.

Factors that may regulate productivity are the number of times a pair of birds nests per season, the size of the clutch, and egg and nestling mortality. Mortality in older age classes will be shown to remain about the same from year to year; this includes mortality subsequent to the age of five months. All the causes of mortality (p. 266 ff) have been found to operate independently of population density. Actually, clutch-size is the only one of these influential factors that has been found to be related in some way to density.

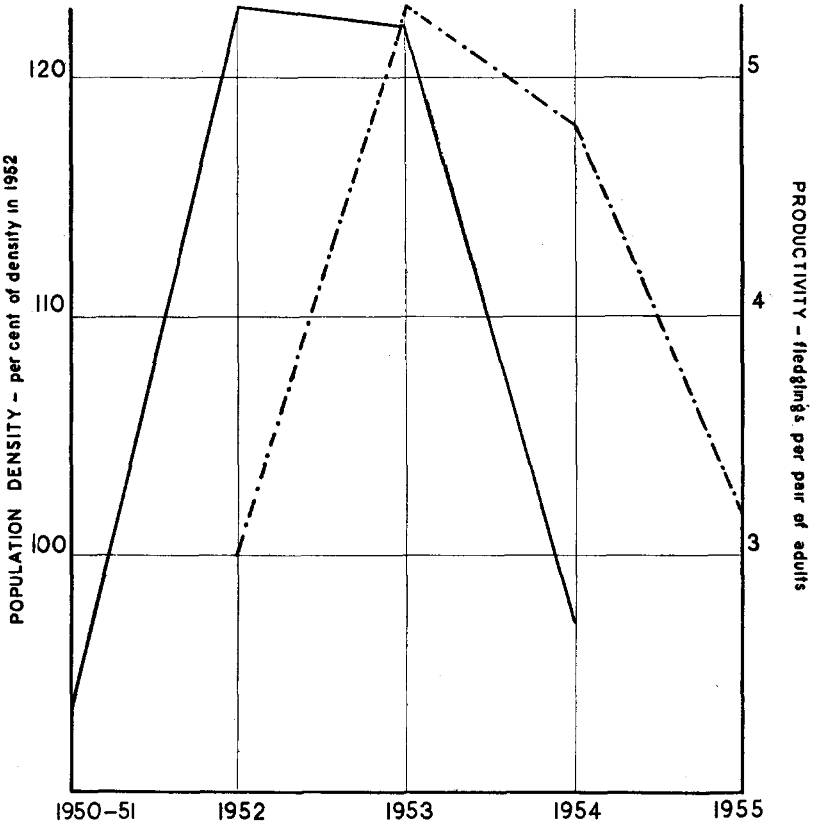

Fig. 2. The relationship between population density (broken line) and productivity (solid line) in salt marsh Song Sparrows.

The relationship of breeding density to clutch-size is examined in figure 3. The ordinate on the left presents population density in terms of the density recorded for 1952; the ordinate on the right presents clutch-size in terms of percentages of the figures for 1952. There is a tendency for clutch-size to increase or decrease inversely as density decreases or increases. This relationship has been noted once before in birds, among Great Tits, by Kluijver (1951:79ff). Kluijver was able to relate this variation in clutch-size to productivity ("fecundity"), and thus was able to say that it was a self-limiting aspect of the numbers of a natural population. In salt marsh Song Sparrows the situation is not at all equivalent, for annual variation in clutch-size is not related to annual variation in productivity (table 9). Moreover the variation in mean clutch-size is of such limited nature that by itself it could hardly affect productivity relationships in successive years so that they would be considered significant by any statistical standard. Thus a curious situation arises: with a probable inverse relationship existing between density and clutch-size it is not possible to say that the relationship has any significance, because of the absence of relationship between productivity and clutch-size (table 9).

Whether or not it lacks significance in the present population, it is of interest to note in this case that the inverse correlation between clutch-size and population density exists in yet another wild population. It is always possible that this relationship as seen here is a remnant of a once-important adaptation in Song Sparrows that, for purely local reasons on salt marshes, has ceased to have any meaning in a populational sense.

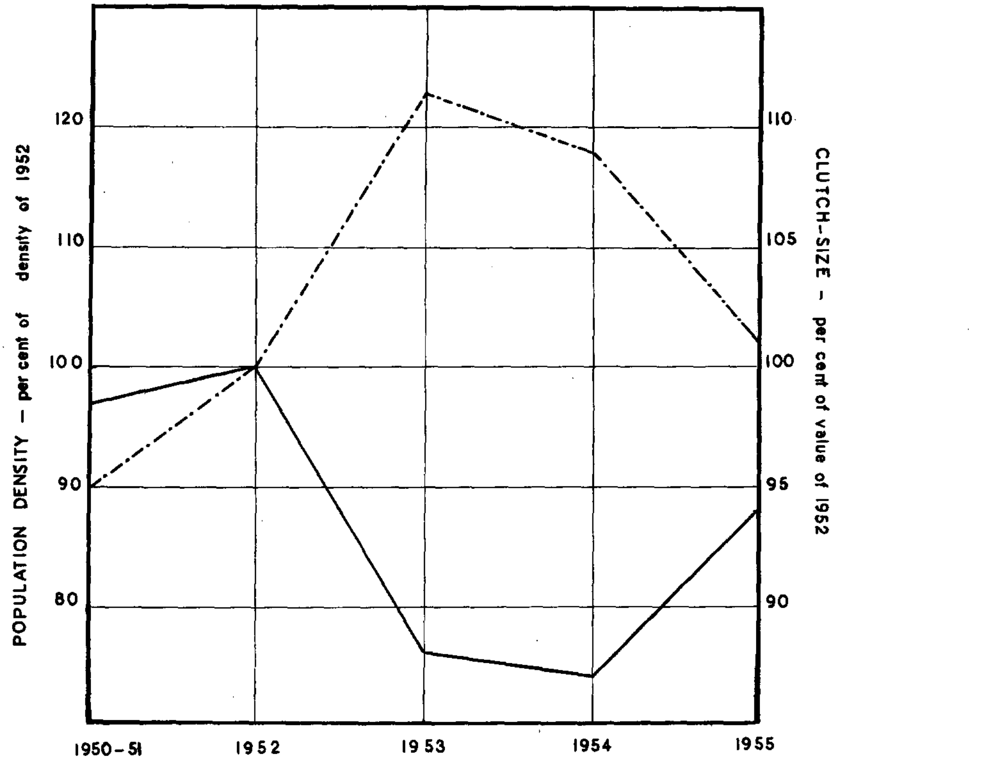

Fig. 3. The relationship between population density (broken line) and clutch-size (solid line) in salt marsh Song Sparrows.

The foregoing considerations in addition to those discussed in relation to territoriality, dispersal, clutch-size, and mortality make possible a generalized graphic representation of factor interactions in the regulation of density in salt marsh Song Sparrows (fig. 4). In am indebted to Ray F. Smith and Frank A. Pitelka for invaluable aid in preparing this diagram. The associations at the top of the diagram are those that occur within the population, primarily as connected with the territorial habit. Those at the bottom show the entrance of factors extrinsic to the population. There is an attempt to classify the relationships into three categories: one of lesser, or intermittent effect, another of consistent but secondary importance, the other of major significance. This is indicated by the width of the arrows. "Biotic fluctuation" and "food" may be termed the condition of the marsh, or, that which determines the number of useable territories in any year. Dispersing juveniles are easier prey for hawks and owls than are the non-mobile members of the population. The remainder of the relationships have been discussed elsewhere.

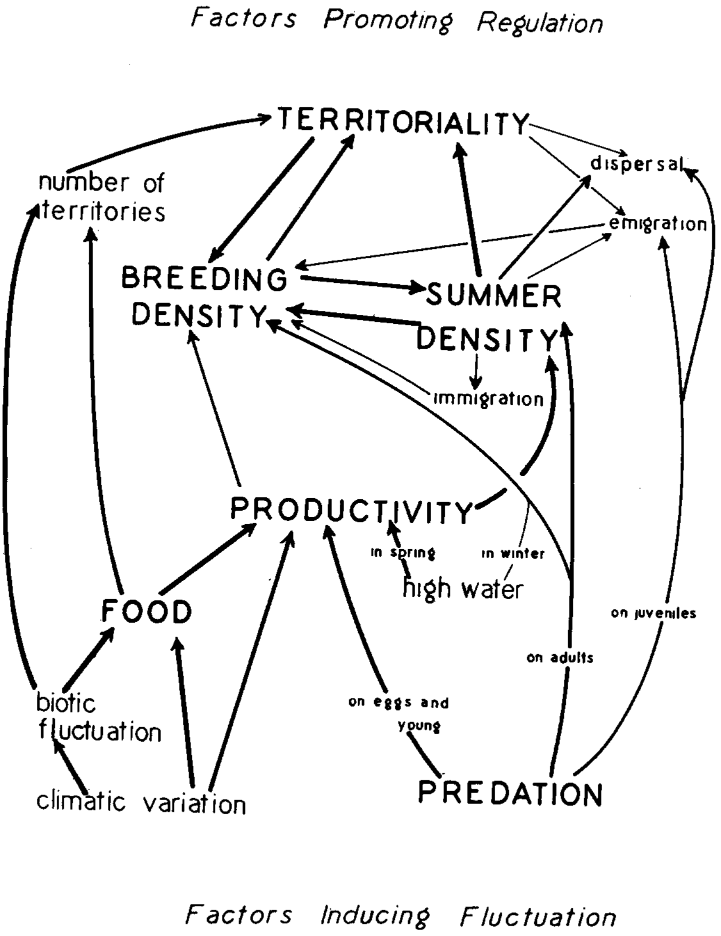

Fig. 4. Factors influencing population density in salt marsh Song Sparrows.

AGE STRUCTURE

Five factors influence the age structure of a population: natality rates, mortality rates, distance of juvenal dispersal, and rates of immigration and emigration. The size of any of the age classes in the population can be modified by changes in any of these five factors. Accordingly, within a population there can exist varying age structures at different times and places. These variations in time no doubt occur in such fashion as to permit a general picture of the age groupings within the population to be drawn. The material presented below is such a generalization, but it is not intended thus to minimize the importance of the dynamic nature of age structure, in particular the pattern of regular fluctation associated with the annual cycle. Since my techniques were not sensitive enough to follow such fluctuation, I cannot indicate with any assurance either the direction or amplitude of change that may have occurred during the time I spent observing these birds.

In this section the foregoing factors in age composition will be examined along with what I call "productivity." Productivity is a function of natality rates and immediate post-natal mortality.

Natality rates.—By natality rate I mean the average number of eggs laid per pair of adult song sparrows per season. This is exactly equivalent to the "fecundity" of Kluijver (1951:79), although my emphasis is on the basic rate of birth rather than on productivity. I use the term "natality" for these birds because of its parallel usage for mammals in being the point in an individual's life when extra-maternal existence begins. Some authors have considered natality in birds to occur at hatching, and there is good embryological justification for this usage, the terms for both mammals and birds then being practically synonymous. But prior to hatching in birds a great deal of mortality occurs from the point of view of the population, and I prefer to consider natality as occurring at laying.

The year 1953 showed the highest natality rate for the three years. This was due chiefly to the favorable environmental conditions that allowed the birds to initiate breeding early in the year so that the average total number of nests per pair was the highest recorded during the course of observations. This high natality rate was reached in spite of a low figure for average clutch-size. Indeed, as can be seen from table 3, natality is unrelated to annual variation in clutch-size. Natality fluctuates independently of any other aspect of this population. Accordingly, natality rate is of itself an unimportant datum of reference in this population. However, it is an important element in "productivity"; this is discussed later.

Table 3

Natality Rates in Salt Marsh Song Sparrows

Year	Clutch-size	Mean number nests/pair/year	Mean number eggs/pair/year
1952	3.42	2.5	8.5
1953	3.04	3.0	9.1
1954	2.91	2.5	7.5
1955	3.23	2.5	8.0
Mean	3.14	2.6	8.2

Mortality rates.—We may now turn to data on and the calculated rates of mortality for some of the age classes in this population. Field observations were most complete in the younger age groupings of the population, especially the egg and nestling stages. In the later stages there is error resulting from the use of small samples which is not calculable. This is particularly true of the mortality rate in the first year of life as calculated from observations of disappearance of banded young; by this means the total mortality in the first year of life for these birds appears to be about 90 per cent. Yet other evidence (table 10) indicates that this population, in order to remain stable or to increase slightly, depends on a survivorship of juveniles of about 15 to 19 per cent; mortality for the first year would seem to be around 80 to 85 per cent, assuming equivalence between immigration and emigration.

In both cases the mortality rates were empirically arrived at, that is, the disappearance of a color-banded individual was assumed to indicate the death of that individual. It is obvious that this is not always a safe or accurate assumption. However, in view of the restricted nature of the movement of the adult portion of the population, I feel that the figures on mortality based on disappearance of adults are a closer approach to the truth than are the figures on disappearance of first-year birds. Table 4 presents the crude data that are used in the construction of the life table (table 5). Since the sample sizes I dealt with are small and also because of limitations of time, I have had to combine data from two distinct age groups in the total population. These are indicated in table 4 as banding groups "A" and "B." Group A is composed of those individuals that I banded in the nest; the data up to the time of fledging (23 days) are completely reliable, but beyond that time my records contain gaps and there is serious doubt that they reflect an actual situation. Group B consists of birds banded as adults. These individuals were at least one year old when my records on them began. They furnished generally reliable data.

Table 4

Field Data Used in Calculating a Life Table for Salt Marsh Song Sparrows

Banding group	Age interval	Number alive at start of interval	Number dying in period
A	0–13 days	403	108
	14–23 days	295	92
	24–365 days	203	185[1]
B	1–2 years	33	14
	2–3 years	19	8
	3–4 years	11	5
	4–5 years	6	2[2]
	5–6 years	3	2[3]
	6–7 years	1	....

[1] *Not* used in life table. [2] Plus one known to be alive. [3] One known to be alive.

Table 5 presents the life table for adult salt marsh Song Sparrows. The methods used in the construction of this table agree most closely with those used for the "composite life table" as defined by Hickey (1952:8); much of this is implied in the paragraph above. The birds under observation were of various relative and absolute ages at the time of banding, and, presumably, lived under different sets of mortality risks. As is true for most life tables based on natural populations, this table has been constructed assuming that all individuals were born at the same time. Additionally, since the study has been a short one and since birds were banded in all years of the study, some of the

Table 5

A Life Table for Song Sparrows on San Pablo Marsh

Age Interval	Number dying in interval (d_x)	Number alive at start (l_x)	Mortality rate in per cent (q_x)
0–13 days	260	1000	26
14–23 days	247	740	30
24–365 days	393	493	80[1]
1–2 years	43	100	43
2–3 years	25	57	43
3–4 years	14	32	43[2]
4–5 years	8	18	43[2]
5–6 years	4	10	43[2]
6–7 years	....	6	43[2]

[1] Average minimum expected according to table 16. [2] Assumed rate.

individuals are still living. Since these birds are included in the data on which the table is based, it not only presents mortality rates in a hypothetical population but also a maximum set of rates for these hypothetical adults.

The figure of 43 per cent mortality per year for birds older than the age of five months agrees closely with what Nice (1937:168) found to be true for the more mobile, mid-continental, male representatives of this species under "normal" conditions of habitat. Probably the highly sedentary marsh population has a lesser rate of mortality than this, as has been indicated (table 5). At the least it is possible to state that the mortality rates in this population are neither unexpectedly slight nor severe.

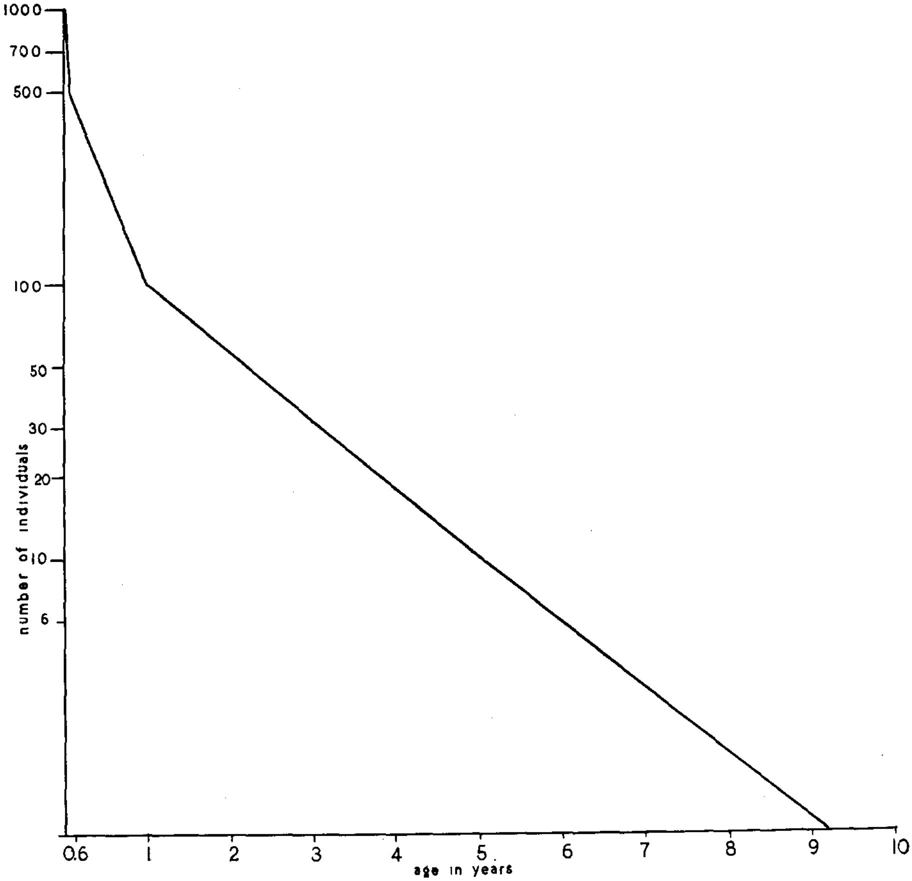

Fig. 5. Survivorship curve for salt marsh Song Sparrows; graphing is semi-logarithmic.

The data describing mortality rates for all the age groups are presented graphically in figure 5. The steep, concave curve describes typically populations that have a large mortality in the youngest age groups, which are abundant. Similar, but steeper, curves have been called "concave J-shaped survivorship lines" and have been thought to be rare among vertebrates (Hickey, 1952:4). However, Song Sparrows in Ohio (Deevey, 1947:298) and the present population appear to be good approaches. Additionally, Sooty Grouse (*Dendragapus obscurus*) in British Columbia (Bendell, 1954), and meadow mice (*Microtus montanus*) in the Sierra Nevada of California (Hoffmann, MS) probably also show a tendency toward this type of curve, and it may be that it is more common among vertebrates than has heretofore been appreciated. On the other hand it is known (Deevey, *op. cit.*) that completely different kinds of curves, representing different mortality relationships, are characteristic of other vertebrates.

A breakdown of all records of mortality for salt marsh Song Sparrows beyond the age of six months has shown that there is no difference statistically between the numbers of birds dying in the period from August to January and those dying in the period from February to July. Nice (1937:174) also found no difference in mortality rates for these two periods of the year, but Erickson (1938:311) noted a 4 to 1 rate of death in winter over summer in the Wren-tit (*Chamaea fasciata*).

Sibling survivorship.—I have examined the data on survival of young birds to the age of one month. Table 6 compares an observed distribution of sibling pairs or triplets that survived to at least one month following fledging to a calculated distribution. This is that calculated by means of the Poisson distribution and is characteristic of random survivorship.

Table 6

Sibling Survivorship in Salt Marsh Song Sparrows

	Number of siblings			
	0	1	2	3
Observed distribution	16	16	6	0
Random expectation	20	11	5	2

The comparison is intended to indicate a high probability that if a bird lives to be two months old, it will more often than not have a sibling surviving to the same age, and that this situation is not merely the result of chance. However, statistical significance by the chi-square test is reached only at the 10 per cent level. Considering the variability inherent in such relationships and the potential for expressing this in small samples, it would be rash to insist that coordinated survival of sibling pairs is an established fact in the present population. But, basically, all that is being said is that if similar genotypes are inherited by siblings then they stand a similar chance for survival to any age, other conditions being equal.

Clutch-size and survivorship.—Table 7 shows the data relating clutch-size to survival. It deals with survival to the age of three weeks, that is, up to the time of fledging. This is probably the most meaningful time at which to consider the influence of clutch-size on survival, as Lack and Lack (1951) have maintained.

The differences in the rates of fledging, representing survivorship to the age of three weeks, are not different enough statistically to warrant assuming that anything other than chance is involved. Under ordinary circumstances it would seem clear that 2-egg clutches are rather a liability in this population. However, most of these clutches were laid in 1954; this was a year of very low fledging success. Since clutches of all sizes are

Table 7

Clutch-size and Survival in Salt Marsh Song Sparrows[1]

Clutch-size	Number of eggs	Number of young fledged	Per cent fledged
2	34	13	38.2
3	180	102	56.8
4	120	68	56.7

---

[1] Data are from 1952, 1953, and 1954.

about equally effective in fledging young, clutch-size plays only a small role in survival of young birds. Lack (1950:281) found that nestling survival in titmice (*Parus*) was nearly the same from both large and small broods. But in the Common Swift (*Apus apus*) Lack and Lack (1951:517) have shown nestling mortality to be higher in large than in small broods when food was in short supply.

With reference to three-egg and four-egg clutches, the fact that they fledge about the same per cent of the total eggs means also that clutches of four should in time become more common in the population if individual control of clutch-size is inherited. Since three-egg clutches exist at all, and are in fact twice as common as clutches of four, there must be some environmental factor or factors favoring the production of three-egg sets. Or, if any inheritance of a tendency to produce the parental clutch-size exists, it is not so strict that the relationship between clutch-size and the environment is thereby weakened or obscured. This is in accord with the belief that small variation in clutch-size in a population is due to environmental causes that vary year to year, as has been outlined above. Kluijver (1951:74) arrived at the same conclusion following an analysis of differences in sizes of first clutches: "Any individual (hereditary) disposition to lay a clutch of fixed size is not predominating, and adaptation to environmental factors is evidently of great importance."

Table 8

Productivity in Salt Marsh Song Sparrows

	Number of nests		Number of fledglings		Productivity	
Season	Initiated per pair	Successful per pair[1]	Per initiated nesting[2]	Per successful nesting[3]	A[4]	B[5]
1950–51	2.5	0.84	0.82	2.50	2.05	2.27
1952	2.5	1.90	2.35	3.04	5.87	5.64
1953	3.0	2.25	1.74	2.32	5.22	5.23
1954	2.5	1.05	1.12	2.46	2.80	2.64
1955	2.5	1.65	1.48	2.30	3.70	3.79

---

[1] Number of nests x per cent of successful nests. [2] A nest in which at least one egg was laid. [3] A nest in which at least one fledgling was produced. [4] Number of fledglings per nest x number of nests initiated. [5] Number of fledglings per successful nest x number of successful nests.

Productivity.—By productivity I mean the number of fledglings produced per pair of breeding adults per year. Table 8 presents the data on productivity. Productivity is calculated in two ways. That the results of both agree closely for any one year is in part a reflection of the fact that both methods have two common bases: the total number of fledglings and the estimated number of nestings initiated. But the concurrence of the figures on productivity for any one year argues for the basic worth of these means of calculating the number of fledglings per pair per year.

I believe that this estimate of productivity is for salt marsh Song Sparrows a more reasonable one than is the use of the total egg production per pair per season (the

Table 9

Clutch-size, Natality, and Productivity in Salt Marsh Song Sparrows

Year	Clutch-size	Natality[1]	Productivity[2]
1952	3.42	8.5	5.87
1953	3.04	9.1	5.22
1954	2.91	7.5	2.80
1955	3.23	8.0	3.70

---

[1] Mean number of eggs/pair/year. [2] Mean number of fledglings/pair/season.

"fecundity" of Kluijver, 1951). We have seen earlier that for this population, variation in egg-production is so slight inter- or intra-seasonally that differences in mortality of the very young age groups are basically the determining factors in yearly productivity; differential egg-production does not enter the picture. This is more clearly indicated in table 9, which shows clutch-size and productivity to vary independently of one another.

Actually, Kluijver's (1951:89) "production" is exactly equivalent to productivity as used here. I made the distinction earlier between productivity and "fecundity" because the recent literature (for example Lack, 1952) has used Kluijver's fecundity rate as the major indication of reproductive intensity for the Great Tit. This has been the case because the inverse correlation betwen fecundity and population density is stronger than that between production and density, although the latter is apparently just as real.

It is likely that with greater variation in clutch-size, as is found in the Great Tit, the use of "fecundity" is an accurate reflection of production of young in a population. This is especially true where there is no great fluctuation in the pre-fledging mortality from year to year, as is perhaps more likely to be true in a hole-nesting species.

The figures on productivity enable a calculation of survivorship in the first year of life to be made; it will be recalled that the empirical data on survival in this age class were deemed unsatisfactory due to difficulty in finding all the surviving birds of any one year subsequent to their dispersal. Table 10 allows another approach; it may be termed a replacement table. The left-hand column lists "corrected productivity," derived by multiplying the yearly productivity per pair by 50 pairs. Since we know from the average annual adult mortality rate that there will be 43 per cent mortality among these 50 pairs in a year, they will require 43 replacements from the crop of young Song Sparrows they produced. The various survivorship rates in table 10 show, at any intersection, the number of individuals surviving after one year. For example, in 1952 the productivity was 290 young per 50 pairs of adults and in the following year the population had increased by 24 per cent; about 70 young of the 290 had survived, a rate of 24 per cent. In 1953 the productivity was 260 young and the following year's population density was not changed significantly over that of the previous year; the survivorship rate was thus about 17 per cent. In 1955 the population declined by 14 per cent following productivity of 140 young per 100 adults; survivorship must thus have been a little over 20 per cent.

Table 10

A Replacement Table for Salt Marsh Song Sparrows

	Rates of productivity	Survivorship rates in per cent 15	16	18	20	25	30
1954	140	21	22	25	28	35	42
Mean	230	35	37	42	46	53	69
1953	260	39	42	47	52	65	78
1952	290	43	46	52	58	72	87

Survivorship in the first year of life for salt marsh Song Sparrows is seen to fall somewhere around 20 per cent per year, if the population is to remain constant, that is, if it is to fluctuate with low amplitude about a mean value. This is close to the rate Nice found for song sparrows in Ohio, but a departure from rates found for species of birds that migrate. von Haartman (1951:47) found a 27 to 30 per cent replacement was necessary for the Pied Flycatcher (*Muscicapa hypoleuca*).

MORTALITY FACTORS

We have seen that there are two distinct groups of song sparrows on the salt marsh with respect to mortality rates. The same division is maintained when the agents of mortality are considered. In the egg and nestling group, which suffers about 50 per cent mortality in a period of a little more than three weeks, the major mortality agents are rodent predators and high tidewater. Subsequent to fledging the expectancy for further life rises until a relatively constant rate of mortality holds effect; this rate is about 43 per cent per year and operates on adults and probably on birds older than 6 to 8 months. The major mortality agents for this age group are, or appear to be, Marsh Hawks and Short-eared Owls; there are doubtless others, but these are notoriously hard to detect and have not been observed in action.

Table 11

Egg and Nestling Mortality Among Song Sparrows on San Pablo Marsh

	1950–51 N = 54		1952 N = 107		1953 N = 140		1954 N = 102		1955 N = 101		Total N = 504	
Agency	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
Predation	15	27.7	11	10.2	35	24.8	23	22.5	15	15	99	20.0
High tide water	13	24.0	8	8.5	4	2.8	19	18.6	12	12	56	11.1
Desertion	7	12.9	3	2.8	3	2.1	13	12.8	1	1	27	5.4
Storm	....	......	4	4.2	6	4.3	....	......	13	13	23	4.6
Infertile eggs	3	5.5	3	2.8	6	4.3	5	4.9	4	4	21	4.2
Loss of eggs	....	......	5	4.6	2	1.4	2	1.9	3	3	12	2.4
Embryonic failure	2	3.7	2	1.8	2	1.4	2	1.9	2	2	10	2.0
Cowbird	....	......	....	....	....	....	....	....	5	5	5	1.0
Totals	40	74.0	36	33.5	58	41.2	64	62.7	55	55	253	50.7

Table 11 lists the major causes of death and their relative importance in several years for the youngest age classes of Song Sparrows. Infertile eggs are included in this list; haploid mortality, that is, death of an unfertilized ovum, is just as effective as the diploid. The birds never replace an infertile egg with a fertile one, and thus the productivity of the clutch is decreased as efficiently as if a predator had removed a nestling. By far the most stable mortality agent is predation. By this I mean chiefly rodent predation. Only in 1952 did mortality due to rodents fall below the 20 per cent level. The next most serious cause of mortality is flooding due to high tidewater; this is of variable, but usually significant, importance. Beyond these major causes of mortality are the lesser factors; although none alone assumes major dimension, in the aggregate they account for more losses than does tidewater. Each mortality agent that appears in table 11 is discussed in turn below.

Predation.—In this category are included all nest losses that clearly were attributable to animals. When a nest that I had been watching was found empty prior to the fledging of the young, and also variously torn and disarranged, I laid the cause to rodent predation. In no instance, however, were rodents actually seen destroying nests but circumstantial evidence was usually strong. One nest was found disarranged, the eggs gone, and in their stead was a fecal pellet of the brown rat (*Rattus norvegicus*), an abundant resident on the marsh. Another nest was found destroyed after rats had found bird seed that I inadvertently had spilled only twenty inches from the nest.

Perhaps of more general significance in establishing rats, and rodents generally, as predators are the details of the drop in population number of the rodents and mammals as a group on the lower marsh in 1952. In that part of the marsh inhabited by Song

Sparrows, rodents were very scarce as indicated by the almost complete absence of cuttings of *Microtus,* fecal pellets of any kind, and nests of *Microtus, Rattus, Reithrodontomys,* and *Sorex,* which normally are easy to find. Probably the low numbers are to be correlated with the extreme wetness of the marsh that spring due to late and heavy rainfall. Most survivors of the mammal populations appeared to have moved higher on the marsh, to areas devoid of Song Sparrows. The old, high marsh is usually only sparsely inhabited by mammals, but in 1952 they found it suitable for living. They occurred there in numbers about three to five times those recorded in years both earlier and later. In 1952 the mortality in Song Sparrow nests that could be attributed to rodents was the lightest in the period from 1950 to 1954; it was half that recorded on the average (table 11).

An attempt to establish mammals other than *Rattus* as predators is difficult. There is one instance of nest disruption known to have been caused by *Microtus,* but in this case the eggs that were in the nest were not eaten, or even broken; it was the nest cup lining that was taken. Likewise little evidence points to *Reithrodontomys raviventris* as a predator; a discussion of the relationship of *Reithrodontomys* to Song Sparrows may be found in Part I (Johnston, 1956) of this report. Shrews (*Sorex vagrans*) may also enter the picture of predation, since it is possible that these mammals may take nestlings, although again there is no evidence.

High tidewater.—Flooding by the tides accounts for the destruction of 11.8 per cent of all eggs laid in an average year. But this does not show the true importance of tidal floods, for mortality due to them may rise to 24 per cent in some years. The water may float out eggs from the nests or may down nestlings. It appears that occasionally nestlings may be killed by exposure to wetness and cold. The eggs of Song Sparrows can stand immersion in salt water for limited periods of time. On one occasion an egg was floated out of a nest and left stranded in vegetation two inches away from and slightly lower than the nest cup. It remained there for an estimated six hours after which time I found it and replaced it in the nest. A young bird hatched from it two days later at the same time that the rest of the clutch hatched, and all young of this nest were fledged at the same time ten days later. It is probable that mortality from wetness and cold varies with the age of the embryo; generally the younger they are the more susceptible they are to chilling.

Desertion or death of female.—Six and a half per cent of the eggs did not result in fledged young because of the absence of the female parent. The absence was due variously to death or causes perhaps of a psychological nature. Probably most of this egg and nestling mortality is due to death of the attendant female parent, but since it is difficult to determine an individual's death, this cannot be unequivocally maintained. Practically all mortality due to desertion occurs in the egg stage.

Storms.—About 4½ per cent of the total mortality was caused by rainstorms. But, more than half of this mortality occurred in one year only (1955); mortality due to rainstorms is intermittent. Death of young Song Sparrows may be effected in at least two ways and also by combination of both. Parent birds cannot easily find enough food for nestlings when it is raining, for insects in the rain here seek shelter or are killed. And the young birds are themselves occasionally killed by the rainstorms, either through dampness, cold and exposure or by direct physical damage inflicted by driving rain or by being blown from the nest by wind.

Infertility.—A little over four per cent of all eggs were infertile. It is possible that some eggs that stopped early in development are included in the total here. If losses due to infertility and to addling are combined, the per cent loss is 6.1. This is very close to the figure of 5.7 per cent loss to these agencies recorded by Nice (1937:146).

Loss of eggs.—About two per cent of the eggs disappeared from the nest before hatching; in all instances the losses were single eggs from clutches of two or more eggs. Probably such loss is due mainly to eggs being kicked out of the nest by the incubating bird when she flushes hastily from the eggs. Thus, much of this type of loss can be laid to my presence on the marsh, for it is unlikely that many incubating females would flush from the nest hastily were I not present (see Skutch, 1954:544). A part of the loss may be due to sporadic theft by *Reithrodontomys.*

Embryonic death.—About two per cent of the eggs failed to develop completely and died sometime before hatching. Mostly the embryos died at about three to six days of incubation, and therefore when I could check them they were decomposed. Accordingly, it was not possible to determine the cause of death of any of these embryos.

Table 12 shows the relative importance of the three major causes of egg and nestling mortality; 41.8 per cent of mortality occurs in the egg stage and 58.2 in the nestling stage. Considering the fact that there are always more eggs from which losses are drawn than there are young, it is apparent that there is significantly more mortality occurring in the nestling stage than in the egg stage. Nice (1937:145) found more mortality occurring in the egg stage, but it seems reasonable to find more deaths among nestlings of altricial birds. Helpless but quiet eggs seem less likely prey items than helpless but squirming or occasionally noisy nestlings.

Table 12

Relative Influence of the Major Causes of Mortality on the Youngest Age Groups of Song Sparrows

	Eggs			Nestlings		
	Number lost	Per cent of egg mortality	Per cent of egg-nestling mortality[1]	Number lost	Per cent of nestling mortality	Per cent of egg-nestling mortality[1]
Rodent predation	31	48.8	20.2	53	58.8	34.2
High tidewater	14	21.6	9.2	30	33.4	19.5
Desertion	19	29.6	12.4	7	7.8	4.5
Totals	64	100.0	41.8	90	100.0	58.2

---

[1] That mortality due to rodent predation, high tidewater, and desertion.

Rodent predation is significantly a greater cause of mortality in both age groups than the other factors examined. Tidewater causes twice as much mortality in the nestling stage; this is probably a reflection of greater susceptibity of the nestlings to being wetted. As has been mentioned earlier, it takes flood water high enough to float eggs from nests in order to result in the deaths of individuals, but a nestling may be killed merely by being exposed to very wet conditions for half an hour. Probably also of significance is the fact that desertion is a greater cause of mortality in the egg stage; the parent presumably has a stronger attraction to the nestling than to the eggs.

Causes of adult mortality are difficult to deal with. The Marsh Hawk (*Circus cyaneus*) is probably the most important predator on adult Song Sparrows. This hawk is present on the salt marsh throughout the year, varying in number from a breeding population of one pair to a winter high of five to seven individuals. Three times I have found feather remains of Song Sparrows that beyond reasonable doubt were the result of plucking by hawks; this is slight evidence indeed, but no other hawks occur on the marsh. Known takers of small passerines that have been seen in the area are the Sharp-shinned Hawk (*Accipiter striatus*), Peregrine Falcon (*Falco peregrinus*), Merlin (*Falco columbarius*), and Sparrow Hawk (*Falco sparverius*). These hawks have been seen only to pass through, or over, the marsh. Doubtless they do hunt on the marsh to some extent, but they apparently represent only a small agency of mortality to Song Sparrows.

Another predator on adult Song Sparrows is the Short-eared Owl (*Asio flammeus*). This bird is present on the marsh from August to April. The average number occurring on the 100-acre plot is five or six; seven or eight probably are present in December and January. Short-eared Owls are known to prey on Song Sparrows since four sparrow skulls appeared in cast pellets of the owls. Four hundred and ninety-one pellets were examined to find the four skulls and it would seem, therefore, that the owl is not a major factor in Song Sparrow mortality.

At the time of the extremely high winter high tides, the Marsh Hawks and Short-eared Owls both hunt extensively in daylight along the *Grindelia* rows that mark the courses of the tidal sloughs. At the time of the highest tides the topmost limbs of the *Grindelia* plants are the only marsh vegetation left exposed above water. It is in this and on floating wood and *Spartina* flotsam that Song Sparrows perch when the water is high. Thus, with other members of the marsh fauna, Song Sparrows are exposed to heavy predation pressure by these hawks and owls at this time of highest daylight tides.

DISCUSSION AND CONCLUSIONS

The means by which the races of the Song Sparrow on San Francisco Bay salt marshes maintain themselves as morphologic entities has been one of the focal points of the present study, as it was also of Marshall's (1948) intensive ecological survey. Additionally, Grinnell (1913:194), Huxley (1942:272), Miller (1942, 1947), Mayr (1942: 249) and von Haartman (1949:83) have all discussed the bay marsh Song Sparrows and their existences as morphologic and ecologic entities. Grinnell and Huxley emphasized the role of ecological preferences or habitat selection in promoting isolation. The remainder, including Marshall, have thought that restriction of movement of individual birds resulting in semi-isolation of the several populations involved, or in isolation by distance (Wright, 1940:245), could account for the ecologic and morphologic diversity now evident. The action of selective forces has always been assumed, and indeed this is essential if divergence of populations is to be accomplished.

These hypotheses will be examined in the light of the data and conclusions of the present study in order to see if they are adequate and whether or not other or alternative explanations seem likely.

Isolation.—Since we are concerned with populations of one species, we have to do not with full isolation but with degrees of partial isolation. There seems to be little question that the short distances involved in the stretches of uninhabitable land between populations of marsh and upland Song Sparrows actually comprise real barriers, hindering the birds in moving easily from one place to the other. The main reason that these short distances mean anything in the evolutionary process in Song Sparrows is that this species is, by and large, not inclined to move.

We have seen that adult members of the population living on San Pablo salt marsh comprise the most sedentary bird population on record. The data presented make inescapable the conclusion that no exchange of members of adjacent populations is going to occur if adult birds such as these make up the populations; the adult Song Sparrows of San Pablo marsh are almost completely isolated from other adult Song Sparrows.

Likewise we may consider the juvenal portion of the salt marsh population to be the most sedentary juvenal segment of a bird population ever found. This is a conclusion based on the extremely short distances that the young birds travel *as a group*. As individuals, however, we have seen that some of them move great distances and that actually these few may well be endowed genetically with a tendency to disperse to considerable distances. It is these individuals that move half a mile or more that serve as links between populations and that in so doing break down slightly the isolation by distance that otherwise separates these Song Sparrow populations. The emphasis here, however, should be on the very high percentage of the juvenal birds that move only slightly; these individuals promote effective spatial isolation.

Selection.—The effects of selection and immigration tend to cancel one another in a given population; since immigration is a negative measure of the degree of isolation obtaining on a population, it is apparent that selection and isolation work together to produce any local differentiation. It has not been possible to assess the force of selection for any particular characteristic of the marsh population. We can see, however, that selection must prevail in order that the semi-isolated marsh population may diverge from upland groups morphologically and physiologically as it has done and is apparently continuing to do.

Evidence in this regard may be found in the degree of difference between adjacent populations of Song Sparrows called *M. m. samuelis* and *M. m. pusillula*. Once the land lying between the Stege and San Pablo salt marshes, to the south and north, respectively, of the city of Richmond, also was a salt marsh (Marshall, 1948:208). There are extant only a few remnants of what was once continuous salt marsh surrounding the Richmond headland; the fractionation of this marsh took place about fifty years ago. Today there are no Song Sparrows living in the area between Stege and San Pablo marsh, but it may be assumed that in all probability fifty years ago individuals representing distal populations of what we now call *samuelis* and *pusillula* were here connected.

Therefore, from a situation of virtual identity, the Stege examples of *pusillula* and the San Pablo examples of *samuelis* have diverged in half a century so that they now are visibly distinct. The differentiation is not marked but it has proceeded in several directions (Marshall, 1948:234–246). One of the strongest characteristics of the south bay populations, that of yellow-colored belly feathers, now occurs in about 25 per cent of the birds at Stege but in only two per cent of the birds on San Pablo marsh.

Also it seems clear that there is selection favoring early breeding on the marsh. In this manner there has been produced the distinctly early breeding populations found on the bay marshes. Late-breeding individuals are yet today at a reproductive disadvantage and will tend to leave fewer offspring than their salt marsh cohorts. This argument supposes that earliness or lateness of inception of breeding is inherited.

Population density.—Density and population pressure will influence the amount and direction of interchange of individuals between populations. In this sense population density has a modifying effect on isolating mechanisms. Movements influenced by density are from the areas of high density and pressure to the areas of low density and pressure. Therefore, a high density on San Pablo marsh would have the effect of tending to turn the tide of movement to areas away from the marsh, providing that these outlying areas are lower in population density than the marsh. Other things being equal, high density of population on the marsh is favored by a high yearly productivity of young; this is favored by early breeding and low egg and nestling mortality.

Habitat selection.—To a certain extent we know that Song Sparrows do select particular habitats over others that they could conceivably live in. Whenever they select a habitat similar to the one in which they were raised, movement tends to be severely restricted. Marshall (1948:249) tells of the shift in numbers of Song Sparrows in the Contra Costa County riparian environments. In these areas, numbers of Song Sparrows increase, presumably by addition of individuals from North-bay upland populations that move out of their breeding habitats when the creeks in those areas go dry in the summer. None of these upland individuals has ever been found in brackish or salt water marshes that lie many miles closer to where the birds started to move. Additionally, of the 2015 skins of the Song Sparrow Marshall looked at, only two were obviously from groups breeding in vegetation types other than the ones in which they were shot.

My data on movements show but one individual, not a bird of the salt marsh, shifting its habitat: a bird reared in a typical riparian situation along Wildcat Creek, but only one-quarter mile from the marsh, which was in view, was found to have dispersed a distance of 660 meters into a fairly typical *Salicornia* habitat. There is no other instance of a shift in habitat by these birds. In those areas where the creeks come through San Pablo marsh, the two vegetation types of willow-riparian and *Salicornia*-salt marsh are juxtaposed. Not much of the original situation is left uncomplicated by exotic plants, but generally the two habitats are in plain view of one another. It is from such areas that one would expect birds to make the shift, as indeed one did. Since the incidence of such shifts is very low, this situation helps to restrict interpopulational exchange.

In the presence of natural selection, it is thus concluded that limited movement, high population density, and habitat selection cooperate to maintain this population as a distinct, recognizable entity.

SUMMARY

This paper is the second part of a report on the population ecology of salt marsh Song Sparrows (for Part I, see Condor, 58, 1956:24–44).

On the study plot, Song Sparrows in a year of medium density existed at about one pair per acre. Along the sloughs, where the birds spend all their time, the density runs from 6 to 10 pairs per acre, depending on the absolute number of birds on the marsh and the complexity of the vegetation available to them. Shifts in density were minor; the largest was a 24 per cent increase in 1953 over 1952. Density was found to vary directly as the preceding year's productivity.

Natality rates varied from 7.5 to 9.1 total eggs per pair per season; these figures are not correlated with clutch-size or productivity. Mortality rates vary from 56 per cent in the first three weeks, to about 80 to 85 per cent in the period of the third to the fifty-second week, to 43 per cent per year for adult birds. A life table is presented. The chances are better than even that if a bird survives to the age of one month it will have at least one sibling also surviving to that age. Clutch-size is not related to survivorship. Productivity varied from 2.0 to 5.8 fledglings per pair per season.

Mortality factors for Song Sparrows include rodent predation, high tide water, death of or desertion by the adults, infertility and embryonic death, and storms. Predation, tidal floods, and desertion cause about 80 per cent of the total mortality to eggs and nestlings. Marsh Hawks and Short-eared Owls are thought to be the most important predators on adult Song Sparrows.

Those aspects of the population structure that favor a strong isolation, a high density of population, and the existence of habitat selection by the birds all favor the maintenance of the integrity and distinctness of the population of Song Sparrows on San Pablo salt marsh.

LITERATURE CITED

Bendell, F. S. J.
1954. A study of the life history and population dynamics of the sooty grouse *Dendragapus obscurus fuliginosus* (Ridgway). Ph.D. thesis, University of British Columbia.

Deevey, E. S., Jr.
1947. Life tables for natural populations of animals. Quart. Rev. Biol., 22:283–314.

Erickson, M. M.
1938. Territory, annual cycle, and numbers in a population of wren-tits (*Chamaea fasciata*). Univ. Calif. Publ. Zool., 42:247–334.

Gibb, J.
1954. Population changes of titmice, 1947–1951. Bird Study, 1:40–48.
Grinnell, J.
1913. Notes on the palustrine faunas of west-central California. Univ. Calif. Publ. Zool., 10:191–194.
Hickey, J. J.
1952. Survival studies of banded birds. U. S. Dept. Int., Spec. Rept. Wildlife, 15:1–177.
Huxley, J.
1942. Evolution, the modern synthesis (New York and London, Harper and Brothers).
Johnston, R. F.
1952. Sixteenth breeding birds census. 25. *Salicornia-Spartina* salt marsh. Aud. Field. Notes, 6:316–317.
1956. Population structure in salt marsh song sparrows. Part I. Environment and annual cycle. Condor, 58:24–44.
Kluijver, H. N.
1951. The population ecology of the great tit, *Parus m. major* L. Ardea, 39:1–135.
Lack, D.
1950. Family size in titmice of the genus *Parus*. Evolution, 4:279–290.
1952. Reproductive rate and population density in the great tit: Kluijver's study. Ibis, 94:167–173.
1953. The life of the robin (London, Pelican Books).
Lack, D., and Lack, E.
1951. The breeding biology of the swift *Apus apus*. Ibis, 93:501–546.
Mayr, E.
1942. Systematics and the origin of species (New York, Columbia University Press).
Marshall, J. T., Jr.
1948*a*. Ecologic races of song sparrows in the San Francisco Bay region. I. Habitat and abundance. Condor, 50:193–215.
1948*b*. Ecologic races of song sparrows in the San Francisco Bay region. II. Geographic variation. Condor, 50:233–256.
Miller, A. H.
1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. Am. Nat., 76:25–35.
1947. Panmixia and population size with reference to birds. Evolution, 1:186–190.
Nice, M. M.
1937. Studies in the life history of the song sparrow. I. A population study of the song sparrow. Trans. Linn. Soc. N. Y., 4:iv+247 pp.
Skutch. A. F.
1954. Parental stratagems of birds. I. Ibis, 96:544–564.
von Haartman, L.
1949. Der Trauerfliegenschnäpper. I. Ortstreue und Rassenbildung. Acta Zool. Fenn., 56:1–105.
1951. Der Trauerfliegenschnäpper. II. Populationsprobleme. Acta Zool. Fenn., 67:1–60.
Wright, S.
1932. The role of mutation, inbreeding, crossbreeding and selection in evolution. Proc. 6th Int. Cong. Genet., 1:356–366.
1940. Breeding structure of populations in relation to speciation. Am. Nat., 74:232–248.

Museum of Vertebrate Zoology, Berkeley, California, August 5, 1955.