

# SURVIVAL AND MOBILITY IN A POPULATION OF PACIFIC COAST SONG SPARROWS (*MELOSPIZA MELODIA GOULDII*)

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The Song Sparrow (*Melospiza melodia*) is one of the most thoroughly studied passerine birds in America, and its life history and breeding cycle are fairly well known. It is also the most polytypic bird in North America, with 31 subspecies currently recognized (American Ornithologists' Union 1957). Certain nonmigratory populations of Song Sparrows tend to be relatively sedentary, individuals rarely moving far from their hatching sites (Nice 1937, Johnston 1956a). In this report we present evidence that the resident population of *Melospiza melodia gouldii* on the Point Reyes peninsula of California also is sedentary. We estimate survival rates, dispersal distance of juvenile birds, and home range size. We conclude that low vagility is widespread among Song Sparrow populations and discuss its consequences.

## MATERIALS AND METHODS

From May 1966 through December 1970 individuals associated with the Avian Biology Laboratory of San Jose State University banded 2522 Song Sparrows in a capture-recapture study of the granivorous birds at the southern end of Point Reyes National Seashore in Marin County, California.

The study area, adjacent to the Pacific Ocean, varies in elevation from 60 m at the top of the cliffs directly above the beach, to 300 m. The study area is approximately 200 hectares, of which about 130 are suitable habitat for Song Sparrows. Most of the area is covered by Northern Coastal Scrub (Munz and Keck 1959). The most common shrubs are *Baccharis pilularis*, *Artemisia californica*, and *Rhus diversiloba*. Parts of old marine terraces at 60 m and 180 m elevation were cultivated, and the rest of the area was grazed by livestock for many years prior to 1966. Since then, these areas have begun to return to their natural state.

Mean monthly air temperatures range from 4 to 15°C. Daily summer temperatures typically range from 8 to 18°C and winter temperatures from 3 to 10°C. In winter, air temperature frequently drops to -1°C on slopes facing away from the ocean. Almost all rain falls from October to April with annual totals of 60 to 125 cm during the years of this study. Fog is common, especially during the summer months.

Birds were mist-netted or captured in grain-baited Glenhaven-Standby Potter traps placed in an approximate 100-m grid in all suitable habitat. Altogether, 192 capture sites were used during the study, but not all were operated regularly.

Every bird was banded with a United States Fish

and Wildlife Service band. At each capture, age, sex, location, weight, molt, and reproductive condition were recorded in the field. We used plumage, degree of skull ossification (Norris 1961), and presence of a cloacal protuberance (adult males) or brood patch (adult females) to classify a bird as a juvenile (in its first calendar year) or adult, if aging was possible.

## RESULTS

### SURVIVAL

Survival, as used in this report, means survival from one breeding season to the next and is estimated from the proportion recaptured the following year. Females with brood patches were first captured in March, so any bird captured after 1 March was considered to have survived to the beginning of the breeding season of that year.

*Adults.* Data for all adults of known sex were analyzed together and overall survival rates estimated. Estimates of survival rates ranged from 0.39 to 0.58 over the four years, with a mean of 0.45 (table 1). Survival rates for males and females were not significantly different ( $P > .05$ ; test for equality of two percentages, Sokal and Rohlf 1969) except in 1966 ( $P < .01$ ) when the difference probably was due to small sample size.

Survival was independent of age after the birds had lived one year. Over the four years 49% of 173 one-year-olds, 43% of 67 two-year-olds, and 50% of 12 three-year-olds survived until the next breeding season. These values are not significantly different ( $P > .05$ ).

*Juveniles.* Estimation of juvenile survival is complicated by dispersal. Some juveniles are not seen the following year even though they have survived. Thus, recapture rates may significantly underestimate the actual survival rates if many juveniles disperse from the study area.

Juveniles recaptured after 1 March were considered to have survived to the breeding season, though not necessarily to have bred. Recapture rates (minimum survival) ranged from 0.16 to 0.32 (table 2). The higher rate for 1966 is significantly different from the other years ( $P < .001$ ) and may be due to errors in age determination in the late sum-

TABLE 1. Annual survival rates of adult Song Sparrows at Point Reyes, 1966-1969.

Year	Males		Females		Total	
	N <sup>a</sup>	s <sup>b</sup>	N	s	N	s
1966	27	0.74	18	0.33	45	0.58
1967	89	0.39	52	0.42	141	0.40
1968	99	0.55	77	0.48	176	0.52
1969	112	0.38	65	0.41	177	0.39
Total	327	0.46	212	0.44	539	0.45

<sup>a</sup> N = Number of banded adults in population.  
<sup>b</sup> s = Proportion recaptured the following year.

mer of 1966. Some birds called "juveniles" may have been adults. After 1966, age determination probably was more accurate because field personnel were more experienced, and because degree of skull ossification was estimated. This is reflected by the more consistent survival rates for 1967-69, during which the minimum for juvenile birds was 0.18.

The number of birds dispersing from the study area can be estimated by the method of Speirs (1963). He gave the following equation for estimating the total population, given the adult mortality rate:

$$P_a = P_1 / (1 - S_a) = P_1 / M_a$$

where  $P_a$  = total adult population,  $P_1$  = population of one-year-olds,  $S_a$  = annual survival rate of adults, and  $M_a$  = annual mortality rate of adults. Solving for  $P_1$ ,

$$P_1 = P_a M_a.$$

This means that in a stable population, enough juveniles survive to replace the adults that die. If we consider  $P_a$  to be the total population of banded adults and determine  $M_a$  from survival estimates (table 1), we can calculate  $P_1$ . Calculated, or expected, juvenile survival rates can be compared with the known minimum survival rates (table 3).

The expected survival rates range from 0.14 to 0.30. Again, 1966 is inconsistent, probably for the reasons already mentioned. Over the four years the expected juvenile survival rate was 0.23. The known minimum survival rate was 0.20. The difference estimates the number of birds that have dispersed from the study area. In other words, 256 of 1298 juveniles (20%) were known to have survived, but 296 (23%) were expected to have survived (table 3). The 40 birds unaccounted for are hypothesized to have dispersed beyond the study area. These represent 3% of all juveniles, or 14% of those surviving.

TABLE 2. Known minimum survival rates of juvenile Song Sparrows at Point Reyes, 1966-1969.

Year	No. Juv. Banded	Proportion Recaptured Following Year
1966	137	0.32
1967	373	0.21
1968	279	0.18
1969	509	0.16
Total	1298	0.20

## DISPERSAL

We define dispersal distance as the distance between a bird's hatching site and its point of settlement the following breeding season. We estimated the hatching site by the first capture site for all juveniles banded before 20 June of any year. Restricting the sample to birds banded before 20 June limited the sample size to only 36 birds, but birds banded after 20 June were likely to have moved from their hatching site already. Recapture records showed that movement nearly always had ceased by the following March; therefore, we used the most frequent (usually the only) recapture site after 1 March to estimate the point of settlement.

The distance between banding site and recapture site was measured to the nearest 25 m for each juvenile banded before 20 June. The results are compared (fig. 1) with similar data for a population of Salt Marsh Song Sparrows (*M. m. samuelis*) in the San Francisco Bay region (Johnston 1956a: fig. 9) and for an Interpoint, Ohio population of *M. m. euphonia* (Nice 1937). To facilitate comparison, the Point Reyes data were grouped into 100-m increments from the banding site. The distributions were similar for all three populations; the medians for the Point Reyes, Salt Marsh, and Ohio popu-

TABLE 3. Expected survival rates and known minimum survival rates of juvenile Song Sparrows at Point Reyes, 1966-1969.

Year	$P_0^a$	$P_a$	$M_a$	$P_{1e}$	$P_{1r}$	$s_e$	$s_m$
1966	137	45	0.42	19	44	0.14	0.32
1967	373	141	0.60	84	78	0.23	0.21
1968	279	176	0.48	85	51	0.30	0.18
1969	509	177	0.61	108	83	0.21	0.16
Total	1298	539	0.55	296	256	0.23	0.20

<sup>a</sup>  $P_0$  = Number of juvenile birds banded;  $P_a$  = total population of banded adults;  $M_a$  = annual mortality rate of adults (from table 1);  $P_{1e}$  = expected number of one-year-olds the following year ( $= P_a M_a$ );  $P_{1r}$  = actual number of one-year-olds recaptured the following year;  $s_e$  = expected survival rate of juveniles ( $= P_{1e} / P_0$ );  $s_m$  = known minimum survival rate ( $P_{1r} / P_0$ ).

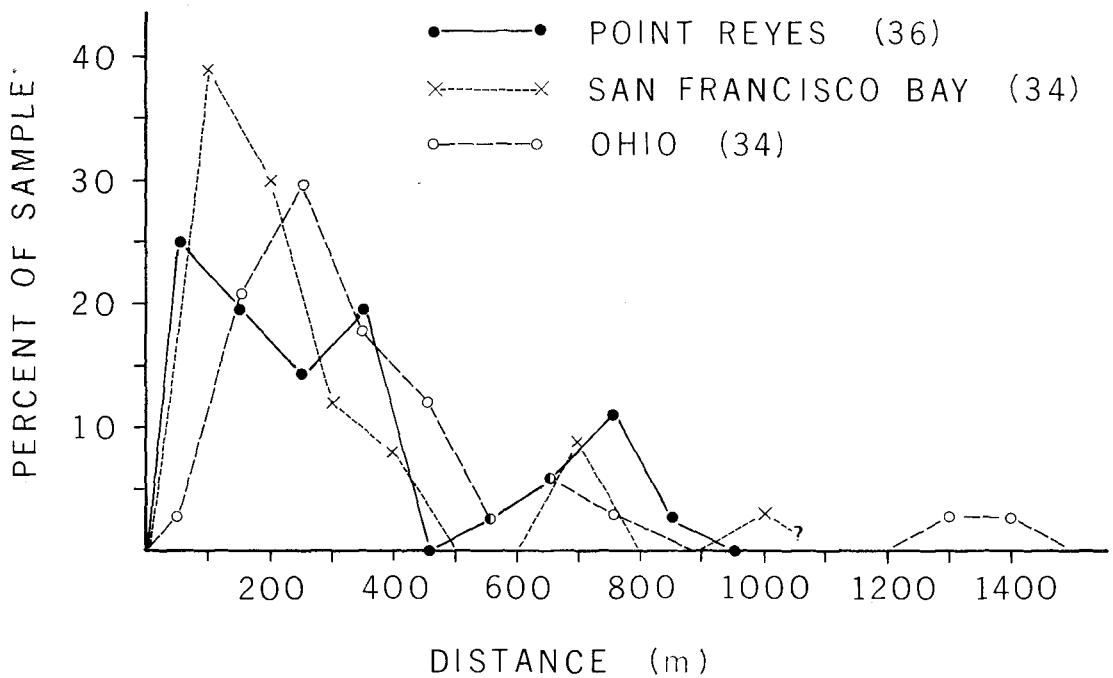


FIGURE 1. Distance from hatching or banding site of juveniles to recapture site the following spring for three populations of Song Sparrows. San Francisco Bay data are from Johnston (1956a); Ohio data are from Nice (1937). Numbers in parentheses indicate sample sizes.

lations were 225, 185, and 265 m, respectively. Of the 36 Point Reyes birds, 78% settled within 400 m of their first capture site while 22% settled more than 500 m away. About 81% of the Salt Marsh Song Sparrows settled within 360 m of their hatching site, and 82% of the Ohio population settled within 450 m.

Ninety-eight juveniles with five or more recaptures but banded after 20 June showed a distribution similar to that in figure 1. The median value of the maximum distance between two sites was 250 m, with 78% moving less than 500 m and 95% moving less than 1000 m. These are estimates of juvenile movement but are not true dispersal estimates because it is very likely that the birds already had moved from their hatching site when first captured. Five of these birds were recaptured 1425, 1725, 2000 (2), and 2175 m from their first capture site, indicating that a few juveniles move substantial distances. This reinforces our belief that a few birds dispersed out of the study area.

#### HOME RANGE

There are two basic methods of estimating home ranges from capture-recapture data. In the first all captures are plotted on a map, and the peripheral capture sites are connected to form a polygon. Either the actual area of the polygon, or the area of some geometrical

figure circumscribing the polygon is used as an estimate of the home range. For reliability, trap sites should be equally spaced and operated on a regular basis. In the second method all captures are mapped and the greatest distance between capture points is measured. This distance is then used either as a simple estimate of the maximum distance an animal may move or as a basis for determining home range area.

We used the maximum distance method to estimate home ranges of Point Reyes Song Sparrows because many traps were not operated on a regular basis and because irregular terrain and vegetation prevented the selection of an "average" shape or area. All adult birds with five or more recaptures were considered. Because the capture records gave no evidence of movement from year to year, all recaptures for adults were considered. Males and females were considered separately, males for the years 1966-1970 and females for 1967-70 (fig. 2). The median values of the maximum distances were 125 m for males and 162 m for females ( $\bar{X}$  = 160 and 239 m, respectively). Forty-two percent of the males, but only 17% of the females moved less than 100 m. This suggests that males may have a greater year-round attachment to a specific territory. Possibly females are more likely to change

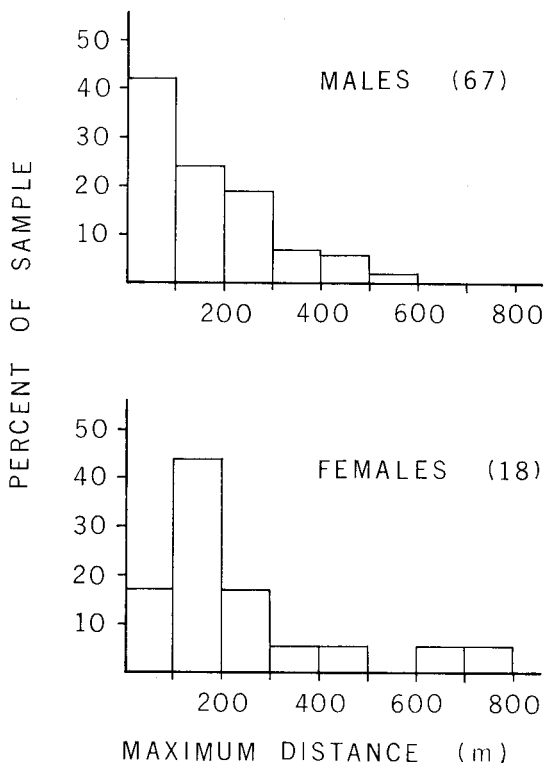


FIGURE 2. Frequency distributions of home range maximum distances for adult Song Sparrows at Point Reyes. Numbers in parentheses indicate sample sizes.

territories after an unsuccessful nesting attempt or if they lose a mate.

Mewaldt and Archibald (1967) estimated mean maximum distances of the home ranges of the same population of Song Sparrows without regard to age and sex as 234 m ( $R = 0-1360$  m). This is close to the value given here for the juvenile dispersal distances, which is expected, as their sample (birds banded May-August 1966), taken during the peak of juvenile dispersal, probably included many more juveniles than adults.

## DISCUSSION

The overall adult survival rates (table 1) are lower than estimates for other Song Sparrow populations. Johnston (1956b) estimated the annual survival rate of Salt Marsh Song Sparrows older than one year to be about 0.57. Nice (1937) estimated the adult survival rate in an Ohio population to be about 0.60 for males and about 0.45 for females. These estimates are for the earlier part of her study; survival was lower during the latter part because of habitat destruction. Tompa (1964) reported survival rates of 0.53, 0.46, and 0.81 for three years in Song Sparrows on Mandarte Island, British Columbia. The lower esti-

mates for the Point Reyes population suggest that either survival was actually lower than in other populations, or that not all surviving adults were recaptured the following year. We do not know which alternative is more accurate, but the home range estimates (fig. 2) indicate that most birds moved very little as adults, making it unlikely that many would leave the study area. The juvenile survival rates (table 2) are similar to estimates by Nice (1937) and Johnston (1956b). Both suggested that about 20% of juveniles survive their first year.

Tompa (1964) recognized three kinds of juvenile dispersal movements. The first, which he called exploratory movements, lasted from the time of independence until the end of the postjuvenile molt in late August or early September. Intensity of movement was related to the number of juveniles in the population. In 1961 when the population density was low, 77% traveled less than 200 m, while in 1962 when the population density was high, only 47% remained within 200 m, and four already had emigrated from the island. The second kind of dispersal, spacing movements, lasted from autumn until spring ending with the establishment of breeding territories. The third kind of dispersal, emigration from the island, occurred at the time of autumnal territoriality and in the spring before the breeding season began. It also was correlated with population density, more juveniles emigrating in years of high density.

Tompa concluded that the density of the population was regulated mainly by juvenile mortality and emigration. Excess juveniles either died or were forced to leave the island. We were unable to determine whether more than one kind of dispersal occurred in the Point Reyes population or if dispersal was related to population density.

The sedentary nature of most of the Point Reyes Song Sparrows is indicated by the median dispersal distance of 225 m for juveniles and the maximum home range distances of 125 m for adult males and 162 m for adult females. However, a few juveniles moved up to 2000 m, or farther. Johnston (1956a) found the same pattern for the Salt Marsh Song Sparrows. Indeed, he called the Salt Marsh population "the most sedentary population of birds yet investigated." He also found dispersal to be nonrandom, with a few juveniles moving farther than expected. He showed that, assuming a Poisson distribution, significantly fewer juveniles than expected dispersed to intermediate distances (300-600 m) and significantly more than expected dis-

persed more than 650 m. He observed the same general pattern for the Ohio population, and wrote that this nonrandom pattern may indicate "a small fraction of the juveniles that are hereditarily endowed with a tendency to disperse great distances" (Johnston 1956a: 42). The Point Reyes population also shows this dispersal pattern, reinforcing Johnston's view that the long distance dispersal of a few juveniles is probably an adaptation by which a certain amount of gene flow is maintained among populations that are relatively isolated genetically.

The juveniles which emigrated from Mandarte Island (Tompa 1964) may be analogous to these long distance dispersers. Tompa suggested that these emigrants were either subordinate males, or those juveniles least tolerant of high population densities.

The polytypic nature of the Song Sparrow is especially obvious in the San Francisco Bay area. Four subspecies are recognized in the region. *M. m. gouldii*, the subject of the current study, is the most widespread, inhabiting fresh water marshes and other moist habitats. *M. m. samuelis*, *M. m. pusillula*, and *M. m. maxillaris* are found exclusively in salt marshes of San Francisco Bay and the adjacent Sacramento River Delta. All have different ecological preferences and usually are separated geographically. These subspecies have been studied morphologically (Marshall 1948a,b) and genetically (Ferrell 1966). Marshall (1948b) found that in general, the degree of morphological differentiation is correlated with the amount of geographical isolation of each population. He found clinal variation in several characteristics, but could not correlate it with any environmental gradients. Ferrell (1966) found significant differences in blood group frequencies among the four subspecies, but found greater variation among populations than among subspecies. He concluded that "variation between races is inundated by heterogeneity between populations" (Ferrell 1966:381). In general, the blood group frequencies could not be correlated with any geographic pattern or morphologic feature. The lack of pattern to this variation suggests that random variation (genetic drift) may be responsible for the differences observed.

Several authors have discussed the significance of genetic drift in Song Sparrow variation (Miller 1947, Marshall 1948b, Ferrell 1966). Miller (1947) using the data of Nice (1937) showed that, due to limited dispersal, the effective size of the breeding

population in Ohio was only about 150 adults. Dispersal estimates have been even less for the Salt Marsh and Point Reyes populations; therefore, it seems safe to assume that an effective population size of about 150 adults is representative of many populations of Song Sparrows. If such a small effective population size is common, then genetic drift is certainly a possible cause of variation among populations.

However, migration (defined here as movement of individuals among populations and subsequent gene flow) tends to make populations more alike and, thus, to counteract the effect of drift. It has been estimated that in the absence of selection, only one to a few migrants per generation, regardless of population size, will prevent differentiation between populations (Wright 1931, Dobzhansky 1970, Lewontin 1974). It seems likely that the few juveniles in each generation who disperse relatively great distances could counteract the effect of drift. If this is true, the apparently random variation such as that found by Ferrell (1966) must be due to natural selection.

The relative importance of random and selective processes in Song Sparrow evolution needs further study. The Song Sparrow, with its many subspecies and small effective population size, is a fertile subject for the analysis of genetic variation.

## SUMMARY

The records of 2522 Song Sparrows (*Melospiza melodia gouldii*) banded from May 1966 to December 1970 on a 200-hectare coastal study area on Point Reyes National Seashore in California were examined to characterize survival, dispersal, and home range.

The minimum annual survival rates were 0.45 for adults and 0.20 for juveniles. The estimate for juveniles is less than predicted, suggesting that some (about 14% of those surviving) dispersed from the study area.

The median dispersal distance of 36 juveniles was 225 m, compared with 185 m and 265 m for two other populations of Song Sparrows. About 78% of the Point Reyes juveniles dispersed less than 400 m, while 22% dispersed more than 500 m. Five juveniles not included in this sample moved from 1425 to 2175 m in their first year, indicating that a few birds move much farther than most. These long distance dispersers probably maintain gene flow between populations.

Home ranges were estimated by measuring the maximum distance between two re-

capture sites. Median values were 125 m for adult males and 162 m for adult females.

The question of whether Song Sparrow variation is due primarily to natural selection or to genetic drift is discussed. Small effective breeding populations make drift a potentially significant factor, but the effects of dispersal may counteract it.

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