VARIATION IN BREEDING SEASON AND CLUTCH SIZE IN SONG SPARROWS OF THE PACIFIC COAST

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In its distribution along the Pacific Coast of North America the Song Sparrow (*Melospiza melodia*) spans about 36 degrees of latitude, from 26°N to 62°N, and ranges altitudinally from sea level to more than 8000 feet. These features of its distribution make the Song Sparrow well suited to a study of its breeding season and clutch size in relation to the climatic conditions prevailing in this region. The data on breeding are examined from the standpoint of increasing latitude and elevation, as this is a convenient way in which to generalize any large-scale variation related to climate.

The raw data on which this report is based consist of 545 records. Most of the data accompany egg sets in oological collections and pertain to locality, date of collection, clutch size, and state of incubation. These records are taken, in large part, from the collection at the Museum of Vertebrate Zoology or from the files of the San Francisco Bay Region Nesting Survey of the Cooper Ornithological Society. Additionally, there are complete, long-term field data for 90 records of *M. m. samuelis* from a salt marsh on San Francisco Bay in Contra Costa County, California. Other records were obtained from I. McT. Cowan, E. N. Harrison, A. P. Marshall, E. Z. Rett, L. B. Silveira, and R. B. Williams, all of whom I thank sincerely. A few records were obtained from Howell (1948:358), Grinnell (1909:230), and Willett (1912:84; 1933:185). I wish to thank Alden H. Miller and Frank A. Pitelka for generous help given me in the preparation of this report.

Table 1 presents a list of the several groups of birds considered here according to general location and size of the sample. The latitudinal groupings reflect in some cases

Table 1

Location and Sample Size of Breeding Groups of Song Sparrows

Group	Latitudinal limits in °N	Number of records Breeding	Clutch size
Baja California	30	......	124
Southern California (*cooperi*)	32–36	113	84
South-central coastal California (*gouldii*)	36.6–37.5	126	86
San Francisco Bay salt marsh (*pusillula*)	37.5	51	48
San Francisco Bay salt marsh (*samuelis*)	38	134	119
North-central coastal California (*gouldii*)	37.5–39	175	143
Oregon-Washington	41–50	43	26
Sierra Nevada (*fisherella*)	37–39	32	32
Alaska	52–62	20	17

the boundaries of morphological races of Song Sparrows on the Pacific coast, and when this is so the name of each race is given. The racial names may refer to real groups, but they do not imply that specimens were taken and identified racially for this study. The racial taxonomy used here is that of Marshall (1948:255).

The dates presented here represent the date of completion of the clutch for each record. Except for field records for which laying or hatching was under observation, the method of figuring the date of completion of the clutch was essentially that of Lack (1946:99), assuming an incubation period of 12 days for all forms of the Song Sparrow discussed here. Thus, a number of days was subtracted from each record according to the given state of incubation; in those cases for which the state of incubation was not indicated six days was subtracted from the record.

The data for a few of the groups were gathered over more than fifty years, through great variation in annual weather conditions, and it may be assumed that approximate extreme dates are represented. In my experience early dates are fairly readily determined for Song Sparrows, but the end of the nesting season is difficult to note, the few late nesting individuals being able to escape detection in the heavy vegetation of July. Therefore, of the extreme dates cited here, the late dates are more probably subject to error.

Certain shortcomings of oological collections have been noted by Lack (1946:99). These consist generally of an inconsistency in the time of collecting and a favoritism for the larger clutches obtainable in mid-season. I have assumed that bias introduced in this manner is minimal since most of the collectors whose material is used here were usually active throughout the season and collected all complete sets of eggs that were found, regardless of the size of the clutch.

BREEDING SEASON

Length.—The data indicating the span of the breeding season are summarized graphically in figure 1. From south to north the season starts progressively later and concomitantly becomes shorter. In southern California the season may start by the second week in February and extend for some five months, and 500 miles north it may start one month later and extend for only three and one-half months. Under more severe climatic conditions the season may extend for but ten weeks, as in the Sierra Nevada, or for about seven weeks, as in the Alaskan Peninsula and Aleutian Islands.

Peak.—Each of the groups shown in figure 1 may be said to have a clear breeding peak or peaks. North from latitude 36°N the peaks occur later in time, and, with the compression of the season, tend to cluster more closely about a modal date. The later peaks of the populations in southern California (*cooperi* and south-coastal *gouldii*) apparently illustrate a tendency already noted among passerines (Baker, 1938:562); that is, the height of the breeding season occurs later at more southerly latitudes than at middle latitudes, although the beginning of the season stretches earlier into the year the lower the latitude. The Song Sparrow race *rivularis* in Baja California at latitude 26°N also has a late peak; according to Bancroft (1930:36) the height of the season is in late April and May.

The earliest nesting peaks are found in the salt marsh races *pusillula* and *samuelis* on San Francisco Bay. It seems possible that these early nesting peaks represent an adaptation to salt marsh conditions since they occur more than two weeks earlier than the peaks for upland populations (*gouldii*) at identical latitudes and coincide with the neap tides of late March and April. With the bulk of the populations nesting during these low tides, the birds, which must nest close to the ground surface, lose a negligible percentage of eggs and young due to flooding by tidewater.

The north-coast populations of *gouldii* and the birds in Oregon and Washington show what are apparently two nesting peaks. This is probably a reflection of chance variation in small samples; at least larger samples would be necessary before any significance could be attached to the two peaks.

CLUTCH SIZE

Latitudinal variation.—Song Sparrows of the Pacific coast show an increase in mean clutch size with an increase in latitude (table 2) and thus with a decrease in length of season and number of broods. Particularly striking is the fact that the incidence of five-egg clutches north of 40°N is about 25 per cent, whereas south of 40°N it is about 2 per cent. Few clutches of five eggs have been recorded south of 36°N. The populations in the Sierra Nevada are similar to the more northerly, coastal ones and produced the only six-egg clutch recorded in the data presented here.

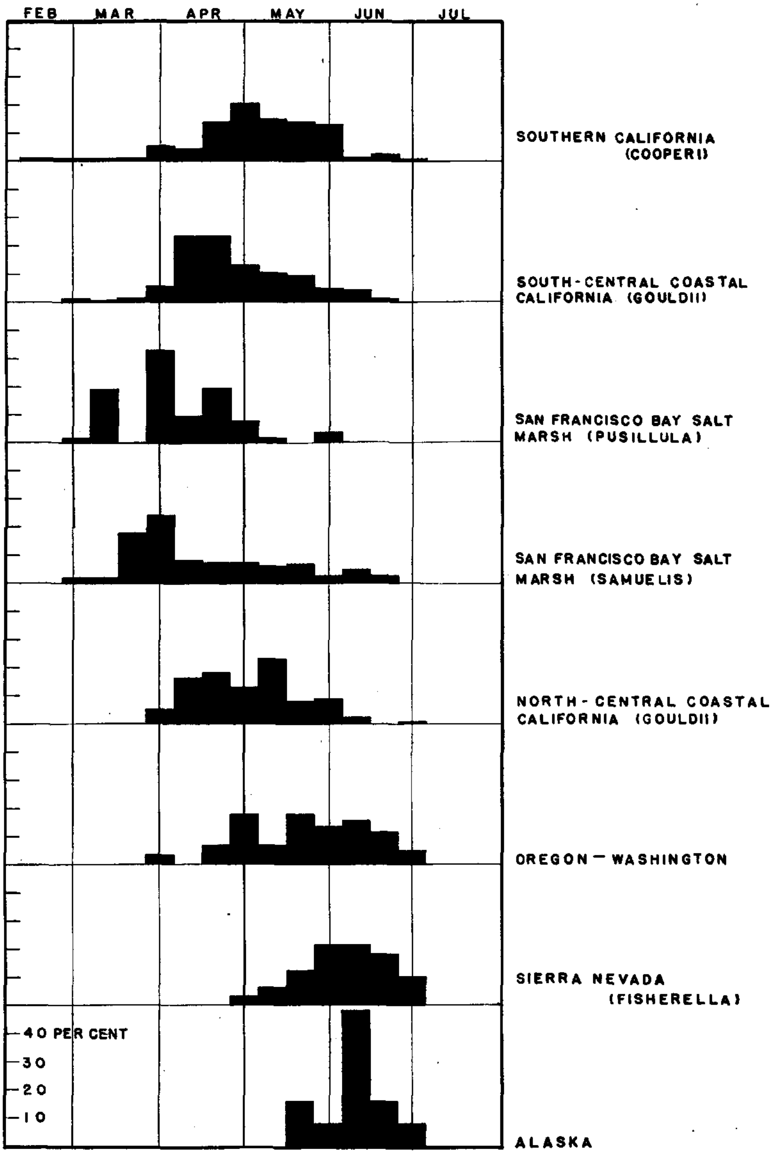

Fig. 1. Breeding seasons, as shown by frequency of completed clutches, in several populations of Song Sparrows of the Pacific Coast. The vertical columns represent 10-day periods, with the 1st, 10th, and 20th of each month as medians.

The small mean clutch size of 3.3 eggs for the birds of the San Francisco Bay salt marsh falls considerably out of the gradient of increasing clutch size in the northward progression. Since two distinct salt marsh populations show this low average it is apparently not the result of chance; rather the indications are that it is adaptive, as Lack's

Table 2

Clutch Size in Song Sparrows of the Pacific Coast

Group	First clutches	Second clutches	Mean clutch size
Baja California	......	......	3.05
Southern California (*cooperi*)	3.74	3.58	3.69
South-central coastal California (*gouldii*)	3.61	3.77	3.71
San Francisco Bay salt marsh (*pusillula*)	3.25	3.40	3.31
San Francisco Bay salt marsh (*samuelis*)	3.10	3.40	3.28
North-central coastal California (*gouldii*)	3.47	3.56	3.53
Oregon-Washington	3.65	4.00	3.81
Sierra Nevada (*fisherella*)	3.90	4.00	3.99
Alaska	4.00	4.33	4.17

analyses of clutch size phenomena indicate. More difficult to understand is the relatively low value, again deviating from the overall gradient, which is recorded here for the northern populations of the race *gouldii*.

Longitudinal variation.—It has been shown previously (Lack, 1947*a*:307) that clutch size increases interiorward over a continental mass. In Song Sparrows at Columbus, Ohio, the average clutch size is 4.15 eggs (Nice, 1937:108), about 0.5 egg higher than at comparable latitudes in non-montane California.

Seasonal variation.—In the salt marsh race *samuelis,* 90 records collected over a four-year period (1950–1953) show a clutch size of 3.1 eggs from the start of the season to April 5, 3.4 from April 6 to May 15, and 3.1 from May 16 to the end of the season. Similar variations in other passerine birds have been chronicled by the Lacks (1947*b*, 1950) and others. All other populations of the Song Sparrow treated in table 2 except those in southern California show a lower mean clutch size for first nestings than for all subsequent nestings through the season; the difference is of the order of 0.2 egg. For these other populations the expected drop-off at the end of the season is not apparent.

BIOCLIMATIC CORRELATION

As indicated above, north of latitude 33° N there is a general and relatively constant retardation in the date of beginning of egg-laying of the Song Sparrow. The retardation seems to conform to the bioclimatic law of Hopkins, a scheme carefully erected to describe the general retardation in biological growing season that occurs with increase in latitude and elevation on all continents. Specifically, the law (Hopkins, 1938:9) states that there is a retardation in season of four days for each increasing degree of latitude, for each five degrees of longitude eastward over a continent, and for each 100 to 125 meters rise in elevation from a given base.

At this point it is pertinent to note that the several investigators of bioclimatics have never agreed as to the absolute length of the seasonal retardation-time coordinates of the altitudinal, latitudinal, and longitudinal components of their "laws." This is due not only to the fact that there were several workers but doubtless also to the resistance of such a complex ecological phenomenon to being rigidly categorized. The various figures of retardation run from 2.75 to 4.87 days (Hopkins, 1938:8). Therefore, in calculating the expected retardation for various localities as shown in table 3 I have given the expectation for both three and four days. Also, in figuring the expected retardation for the station in the Sierra Nevada the expectation is based on three to four days for each 112 meters rise in elevation.

It will be further noted that the few early dates for inception of breeding rather than the later ones when more general breeding is started in the population were used in the arithmetic here; the early dates have the advantage of being more objective, lending themselves better to work of this kind, although they may be possibly less important in nature. In addition, since south of about 36°N the date of inception of general laying occurs later than at middle latitudes those time intervals when most breeding is started would be impossible to use as a basis on which to test bioclimatic relations. But, north of 36°N the relation to climate holds for both the earlier dates and those intervals when most of the breeding is started.

Table 3

Seasonal Retardation and Bioclimatic Correlation of Breeding in Song Sparrows

Station (lat. °N, long. °W)	Elevation	Early date	Retardation in days	
			Actual	Expectation
33, 117.5	....	Feb. 10	....	....
38, 122.5	....	Feb. 26	16	15–20
39, 120	2000m	Apr. 27	76	72–96
40, 83	220m	Apr. 13	62	48–64
48, 120	....	Apr. 1	50	45–60
58, 135	....	May 19	98	75–100

Using all samples, and on the basis of the earliest dates for all localities concerned, the figures in table 3 show that the inception of breeding in the Song Sparrow is retarded about three days for each 100 to 125 meters rise, up to 2000 meters (6200 feet) elevation in the Sierra Nevada, and for each degree of latitude to 38°N, about three and one-half days for each degree to 48°N, and about four days for each degree to 58°N. These results seem to support the bioclimatic generalizations of Hopkins.

As a check on the existence of the "longitudinal retardation" of three to four days for each five degrees of longitude, an interior population at Columbus, Ohio, is found to show a retardation of 62 days, with an expectation from the bioclimatic law of 48 to 64 days (table 3). Since there are no data at hand for stations lying between California and Ohio it is not possible to say whether this correspondence represents part of an overall continental gradient or is sheer coincidence. It is, however, suggestive, and indicates a need for additional investigations of breeding in the Great Plains regions.

Other investigators have found reasonably similar retardation in breeding of birds. Baker (1938) in his survey of latitudinal influences on breeding seasons found a two to three day retardation per degree of increasing latitude in a great number of birds breeding from middle latitudes to the subarctic. Kessel (1953) noted a retardation in breeding of three days per increasing degree of latitude in the Starling (*Sturnus vulgaris*) along the Atlantic coast of North America.

With regard to the handling of the present data it is well to note that although Hopkins allowed for correction factors depending on the edaphic and physiographic nature of the stations under consideration, for the majority of the localities treated here it was not possible to obtain precise information. It will also be noted that no correction for longitude was made for stations running north along the Pacific coast line; I felt that to have done so would not have been a realistic interpretation of Hopkins' rule, for there is no progression eastward across a continental mass in spite of the 17 degrees of longitude difference between Juneau, Alaska, and Encinitas, California.

SUMMARY

1. The breeding season in Song Sparrows is shorter and starts later in the year at higher latitudes as compared with lower latitudes.

2. The peak of the breeding season is earliest at middle latitudes, intermediate at lower latitudes, and latest at higher latitudes.

3. Clutch size increases with increasing latitude, increasing altitude, and decreasing longitude over the North American continent.

4. In at least one race of Song Sparrow (*samuelis*), clutch size is smaller at the beginning and end of the season and larger in the middle.

5. Inception of breeding in Song Sparrows is retarded by three to four days for each degree increase in latitude, each 100 to 125 meters rise in elevation, and probably also for each five degrees decrease in longitude over a continental mass. Thus, in its breeding this species conforms to some set of natural forces subsumed by the bioclimatic law of Hopkins.

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