COMPARATIVE BIOLOGY OF PACIFIC COASTAL WHITE-CROWNED SPARROWS

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A linear series of populations of White-crowned Sparrows (*Zonotrichia leucophrys*) inhabit 1900 kilometers of the Pacific coast of North America, from about Santa Barbara, California, to somewhat above Comox on Vancouver Island, British Columbia. The southern populations are nonmigratory and have been assigned to the race *nuttalli*; the northern populations are largely migratory and belong to the race *pugetensis*. Populations south of San Francisco Bay are found only within a few hundred yards of the beach. From San Francisco and Berkeley to southern Oregon, most populations are restricted to within a few miles of the sea. In Oregon, Washington, and southwestern British Columbia, populations are found on the coast and in the interior valleys west to the Cascades. They are not known to come in breeding contact with the race *gambelii*, which nests from the Cascades of extreme northern Washington (Farner 1958; Banks 1964) to above the Arctic Circle in Alaska and Canada. Also there is no breeding contact with the mountain race *oriantha*, which breeds in small numbers as far west as the Cascades of Oregon and in larger numbers in the Sierra Nevada of California.

The migratory races *pugetensis* and *gambelii* winter in the lowlands of California often in mixed flocks. On the immediate coast of central California flocks containing *pugetensis*, *gambelii*, and *nuttalli* are not uncommon in winter. These flocks also occasionally contain the migratory Golden-crowned Sparrow (*Zonotrichia atricapilla*) in small numbers. Although some apparently "pure" flocks of each race are encountered, the most suitable crowned sparrow habitats seem to be occupied by the three migratory forms inland and by all four forms on the coast.

The most comprehensive accounts of the White-crowned Sparrows of the Pacific Seaboard are those of Barbara B. DeWolfe. (Several of her more important papers appear under the names B. D. Blanchard and B. B. Oakeson.) Of special interest are Blanchard (1941, 1942), Blanchard and Erickson (1949), Oakeson (1953, 1956), and Oakeson and Lilley (1960). The recent detailed analysis of the morphology of breeding populations of all races of *Zonotrichia leucophrys* by Banks (1964) is pertinent and very useful.

It is apparent, especially from the studies of DeWolfe, that the chronology of events in the annual cycle varies with the latitude of the breeding grounds. For example, birds that breed at southern latitudes (*nuttalli*) separate from the mixed winter flocks to take up territory and start nesting while birds that breed at northern latitudes (*pugetensis*) remain in flocks and undergo a prenuptial molt before migration. It is apparent that these two groups are of distinctly different genetic stocks. It has proved difficult, however, to distinguish between the races *nuttalli* and *pugetensis* near the zone of contact.

It has been our objective in this investigation to characterize the array of populations so that we can (1) better understand physiological and behavioral differences between migratory and nonmigratory races of a species, (2) better define the geographical location of the zone of contact between these races, and (3) describe the nature of the gradient between contrasting characteristics of the races.

MATERIALS AND METHODS

The White-crowned Sparrows (*Zonotrichia leucophrys nuttalli* and *Z. l. pugetensis*) used in this investigation were captured on their breeding grounds with mist nets during the summers of 1959 and 1960. Ten populations were sampled each year from along the coast of California, Oregon, Washington, and British Columbia (fig. 1). In 1959 birds were collected at Pismo Beach, Palm Beach, Santa Cruz, Westport, Capetown, and Clam Beach, California; at Frankport and Oceanlake, Oregon; at Ocean City,

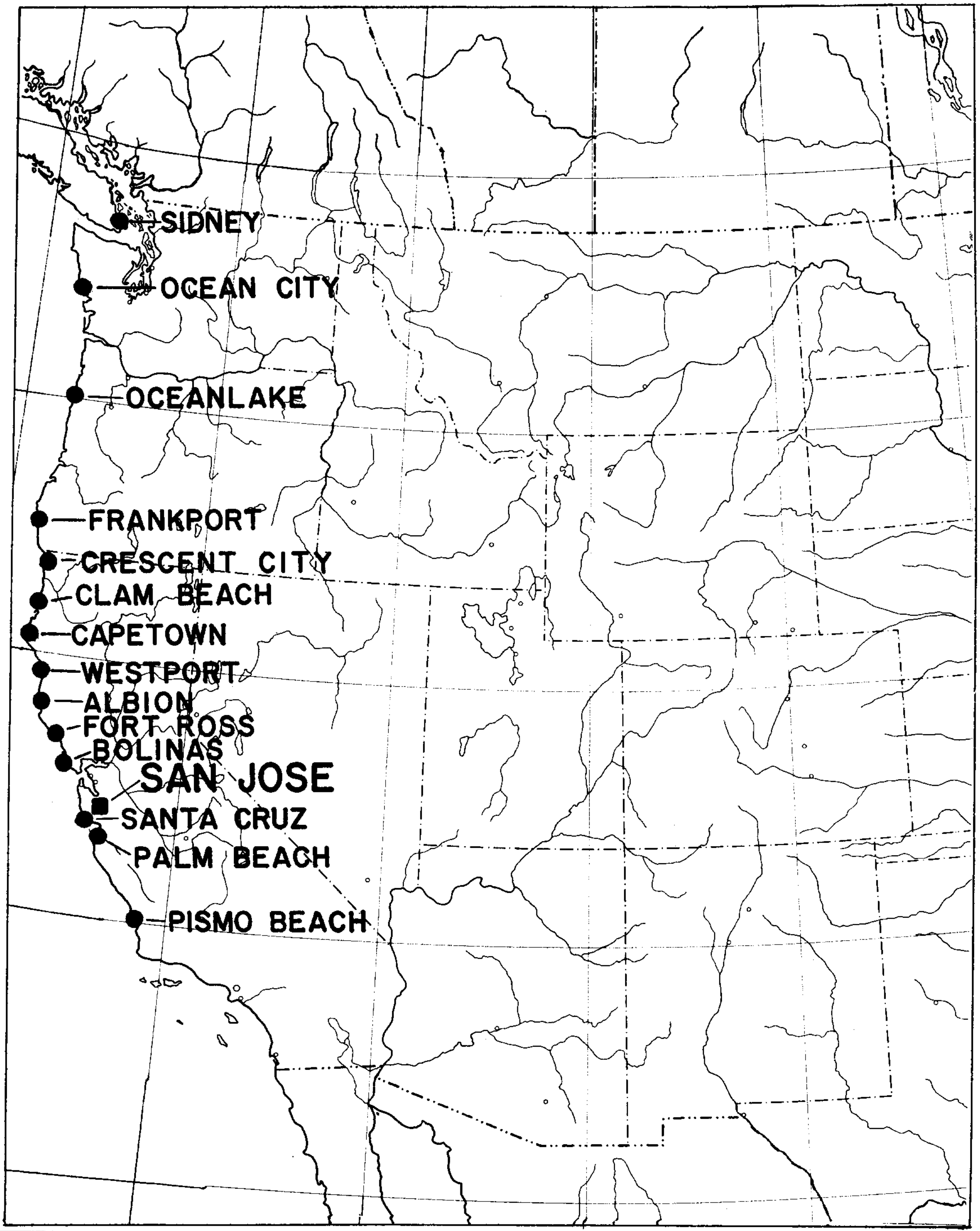

FIGURE 1. Pacific coastal capture sites of White-crowned Sparrows, *Zonotrichia leucophrys*, in relation to San Jose, California.

Washington; and Sidney, British Columbia. In 1960 birds were obtained at Palm Beach, Bolinas, Fort Ross, Albion, Westport, Capetown, Clam Beach, and Crescent City, California; Ocean City, Washington; and Sidney, British Columbia.

The birds captured were adults on territory or adults and immatures that had congregated into small postbreeding flocks on the breeding grounds. Upon capture, the birds were placed in a mobile aviary for cage acclimatization and were transported to San Jose, California. There they were installed in an outdoor aviary on the roof of the Natural Sciences Building of San Jose State College. Unless they were being tested in activity cages, the birds were held as a mixed group in a walk-in aviary 3.6 × 2.5 × 2.0 meters high. The air temperature and photoperiod were those natural to the San Jose area.

Throughout the period of captivity food and water were provided *ad libitum*. The staple food was ground dry dog food, which was vitamin- and mineral-enriched and high in protein content. This was supplemented by a weekly feeding of fresh lettuce, chick scratch, red millet, and grit.

At weekly intervals the birds were weighed and examined for molt. Weights were taken to the nearest half-gram on a balance accurate to one-tenth of a gram. Molt was noted separately for coverts, rectrices, remiges, body, and crown areas. The overall intensity of molt was determined by arbitrarily designating the condition of each bird as no molt, light molt, medium molt, or heavy molt. These designations were then used in the following equation to provide a mean numerical index of the intensity of molt:

$$\text{Molt index} = 10\,\frac{(\text{No. light} \times 1) + (\text{No. medium} \times 2) + (\text{No. heavy} \times 3)}{\text{total number of birds examined}}$$

The percentages of birds molting the central rectrices and those molting the secondary remiges 7, 8, or 9 were also calculated.

At approximately monthly intervals in the spring, laparotomies were performed under general anesthesia (sodium pentobarbital) to determine the extent of gonadal development. Testicular dimensions to the nearest 0.5 mm were substituted into the following equation to determine paired testicular volume: $V = 2\ (4/3)\ (\pi\ ab^2)$ where $a = \frac{1}{2}$ the long dimension and $b = 1/2$ the short dimension. We consider this method to be justified since the right and left testes of *nuttalli* and *pugetensis* are nearly identical in size. In order to reduce the technical error, one investigator made most of the measurements.

In 1959–60 and 1960–61, two birds from each of the 10 capture sites of each year were tested in individual activity cages (41 × 22 × 26 cm) equipped with a centrally located, activity-sensitive perch. The activity cages were adapted from a design of Farner and Mewaldt (1953). The 20 cages were placed side-by-side in a double tier with the birds distributed randomly with respect to their place of origin. Activity was monitored continuously by a remotely located Esterline-Angus graphic recorder in 1960 and by Elmeg digital recorders set to print once each hour in 1961.

We considered carefully the consequences of random placement of birds in the activity cages. Our concern for the effects of social stimulation has been almost entirely retired on the basis of the results obtained. In spite of the random placement, the birds did respond predictably in accordance with geographical origin. In any case, if there were effects due to social stimulation, they would tend to reduce the differences between populations rather than increase them. It is also noteworthy that birds caged individually in the activity cages did not differ materially in weight, molt, or gonadal development from the birds housed as a "flock" in the adjacent large aviary.

Each of the 20 activity cages was monitored continuously for depressions of the centrally located perch. The usefulness of data so obtained as a measure of migratory restlessness (*Zugunruhe*) has been discussed by Farner, Mewaldt, and King (1954). The number of hours of the 24-hour day in which the birds exhibit activity and the temporal placement of these hours is probably accurately shown. The intensity of activity, as reflected by the number of perch registrations per hour, is less accurately determined. This is because individual perch assemblies have slightly different sensitivities and because there is variation in the way individual birds behave in respect to the perch assembly. Direct observations of the birds suggest, however, that most birds behave very much alike. Used with certain caution, we feel that differences in the intensity of activity provide us with useful information.

Esterline-Angus tapes were run at 45 inches per hour from 29 January to 10 June 1960, and for one selected week each in September, October, November, and December of 1960. This permitted detection of nearly every depression of the perch. When activity was so intense that individual perch registrations could not be distinguished, we assigned a maximum value of 15 perch registrations for each $\frac{1}{8}$ inch of tape. Direct observation of birds revealed this to be a reasonable estimate of maximal activity. The reliability of this estimate was supported when, starting in January 1961, we used Elmeg impulse counters programmed to print out hourly the actual numbers of perch registrations. Our counts obtained very tediously from the 1960 tapes appear to be comparable to the 1961 Elmeg records. We have, therefore, combined them for most analyses of activity data for February, March, April, and May.

Activity data for July and August are available for 1960 only, and then on tape that ran at three inches per hour. In this case we were able to justify only a maximum of 15 perch registrations for each two-minute interval on the tape ($\frac{1}{10}$ inch of tape). The resultant maxima of 450 perch registrations per hour are too low. However, the activity patterns are satisfactory so long as it is realized that periods of peak activity are usually too low when compared with periods of peak activity in months when tapes were run at 45 inches per hour.

RESULTS AND DISCUSSION

WEIGHT CYCLE

Free-living *Z. l. pugetensis* trapped and retrapped over a period of several years (1954–66) in population studies at San Jose, California, usually exhibited light fat during the winter months. As they completed their prenuptial molt in late March, and immediately before their disappearance from the trapping sites, most birds deposited moderate to heavy fat. Blanchard (1941) also observed deposition of premigratory fat in *pugetensis* concurrent with a weight increase, later found by Wolfson (1945) to average approximately 3½ grams. *Nuttalli*, on the other hand, as shown in our recent studies at Point Reyes and by Blanchard, generally do not deposit fat nor do they show the vernal weight gain. Most *nuttalli* have already begun nesting in March when *pugetensis* complete their prenuptial molt, become fat, and then in early April make their northward migration from the San Francisco Bay area. Blanchard found that *pugetensis* were lean upon arrival on the breeding grounds in the vicinity of Puget Sound.

The weight data from the birds in our aviary investigations are divided by sex into northern and southern populations (fig. 2). Because more detailed analyses of data on weights proved unprofitable, we have com-

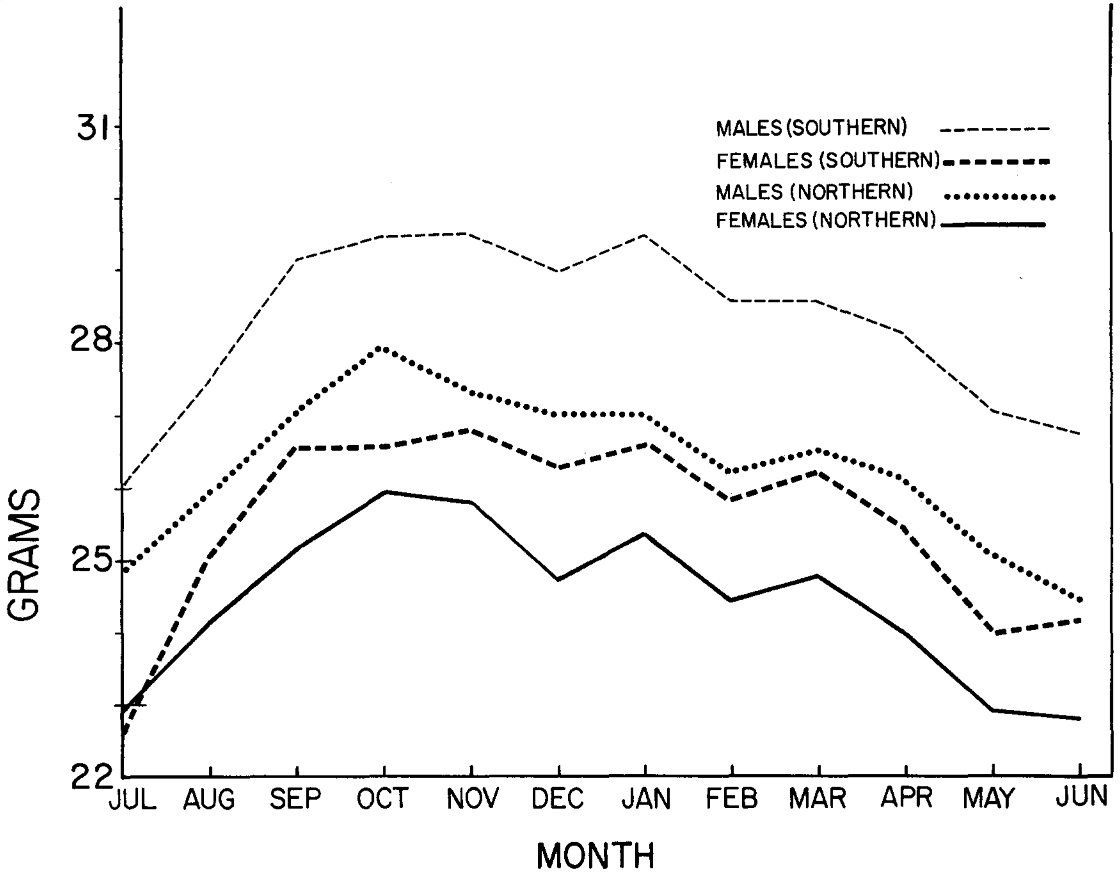

FIGURE 2. Monthly mean body weights (taken weekly) of nearly 200 captive White-crowned Sparrows over a span of two years. Southern birds include those from Capetown southward, and northern birds include those from Clam Beach northward (fig. 1). Approximately 8000 weights are included.

pared mean weights of northern and southern males and females by months only. To exhibit the data better, we have in this instance included the birds from Capetown with the generally larger birds of the southern populations (see fig. 1). The annual cycle of weights by months for both northern and southern birds and for both males and females shows the typical summer lows and winter highs demonstrated for many species of birds by Baldwin and Kendeigh (1938).

During the two years of this investigation only about 10 of our 170 captive coastal birds showed a vernal weight increase that could be attributed to premigratory fat. These 10 were all from northern populations (*pugetensis*) but were otherwise scattered in origin. None of the southern birds displayed vernal fattening. Because the 10 northern birds were asynchronous in the onset of vernal fattening and because these reserves were retained for only a couple of weeks, the statistical effect of these birds on any grouping of weight data was negligible. We had, however, expected northern birds (*pugetensis*) to deposit considerable fat as they completed the prenuptial molt. In adjacent aviaries, *Z. l. gambelii*, *Z. atricapilla*, and a few *Z. l. pugetensis*, all captured at San Jose as wintering birds, became fat as expected and sustained the fat for several weeks. Twenty *Z. l. oriantha* that, like our coastal populations, had been captured on their breeding grounds the previous summer also failed to deposit fat. It appears that some factor or factors associated with captivity interfered with the vernal premigratory weight increase in *pugetensis*. Further speculation on this point seems unjustified. Because we found no significant differences between the weights of birds captured as immatures or as adults, the data are combined.

Birds from our southern populations averaged 1 to 3 grams heavier than birds from the northern populations. Mean weights of males by individual population for the month of December (fig. 3) very closely approximate the data of Banks (1964) for breeding males.

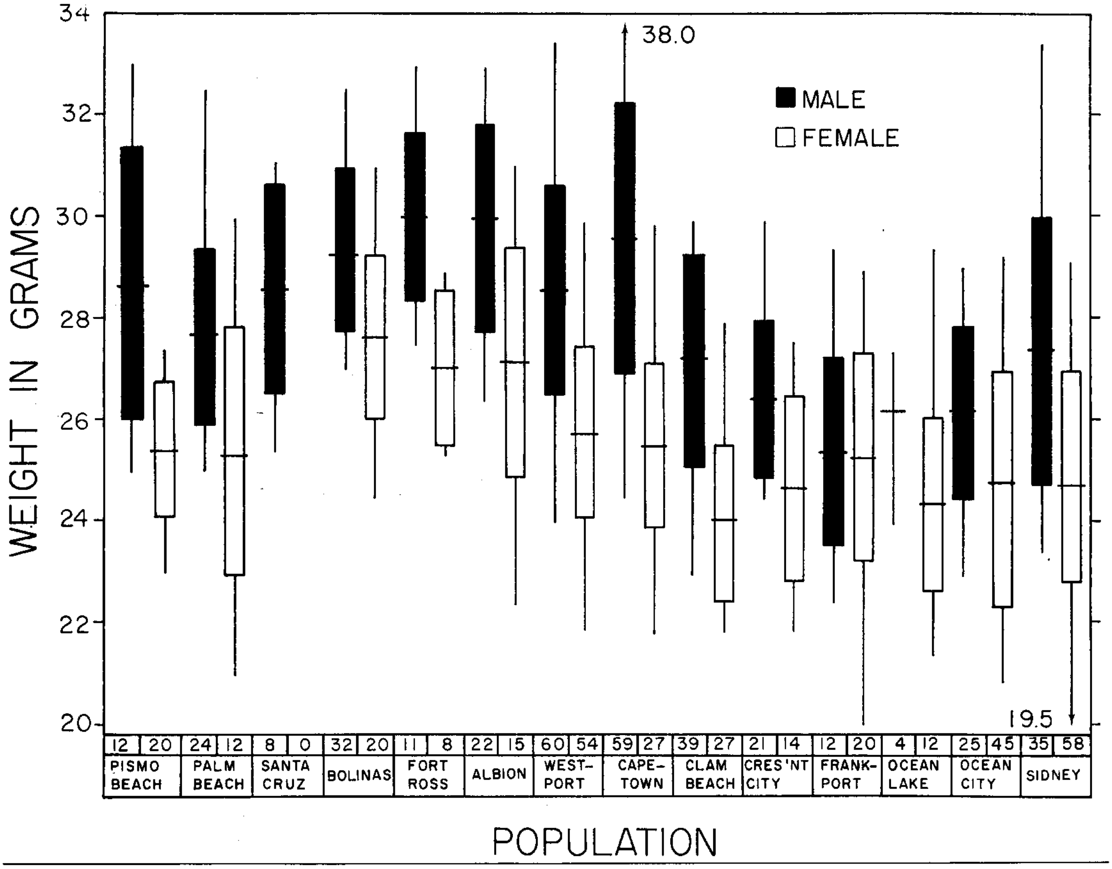

FIGURE 3. December weights attained at San Jose by male and female White-crowned Sparrows from 14 Pacific coastal localities. Mean (horizontal line), standard deviation (rectangle), and range (vertical line) are provided for the total number of weekly weighings (numerals along abscissa) in December.

He found the mean weights from Humboldt (near Capetown) south to be 27 grams or more, and the mean weights of males north of Humboldt to be 27 grams or less. Mean weights of our females from Capetown south were 25.5 grams or more whereas mean weights of females north of Capetown were 25.4 grams or less. In both investigations the division point between large and small birds occurred immediately north of Humboldt (Capetown). The mean weights of males were 1.8 to 4.0 grams more than those of females in all populations except Frankport, from which only a small sample was available.

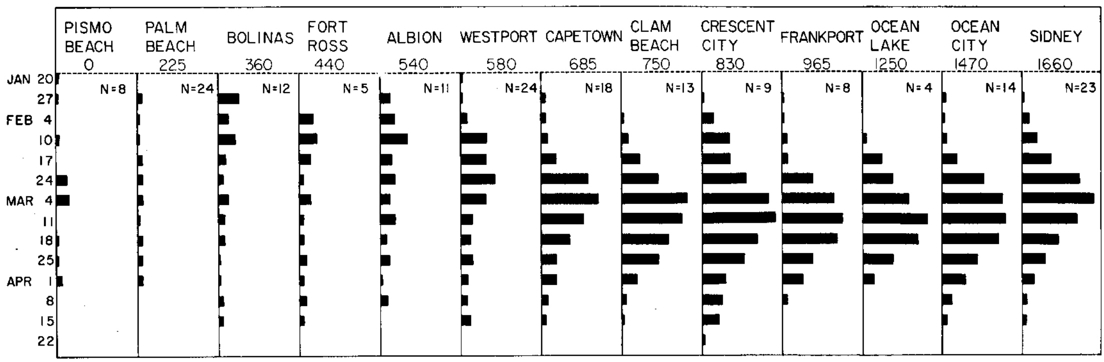

FIGURE 4. Mean intensity of prenuptial molt by weeks in *Zonotrichia leucophrys* from 13 coastal populations held at San Jose in 1960 and 1961. The longest black bars indicate that nearly all birds were simultaneously in heavy molt in that week. Kilometers north of Pismo Beach are shown below each population site.

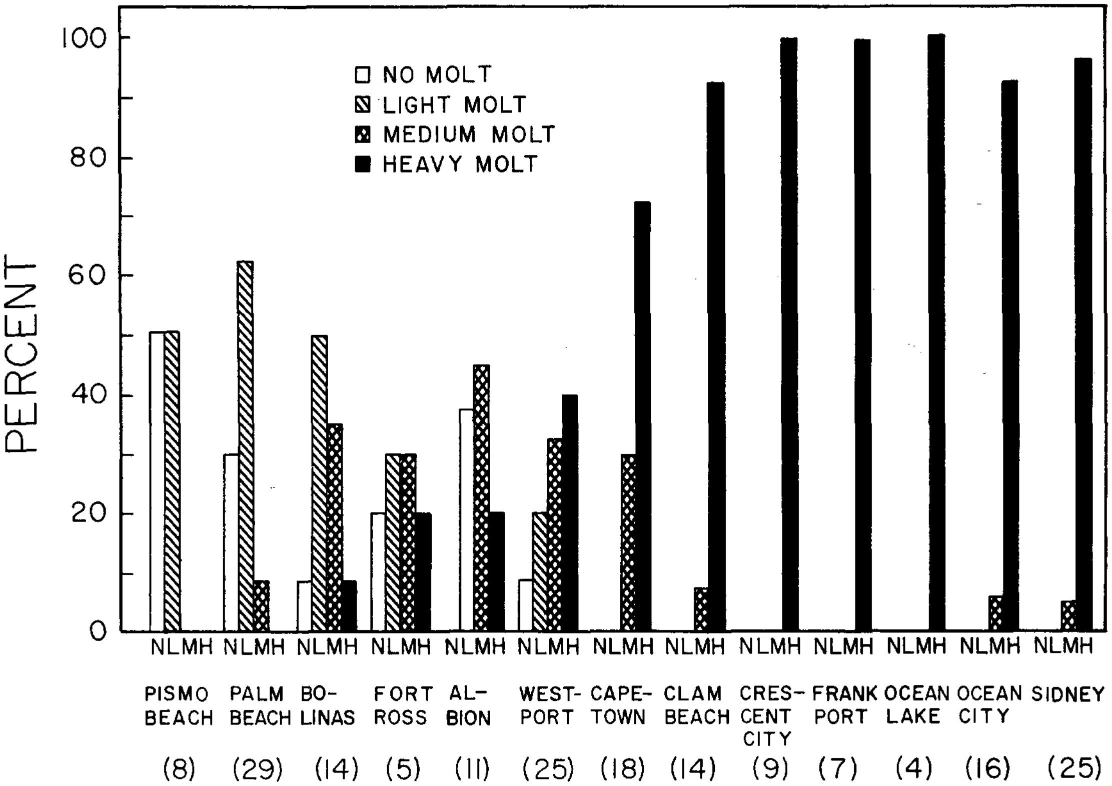

FIGURE 5. Maximum intensity of prenuptial molt attained by individuals from coastal populations of *Zonotrichia leucophrys* held at San Jose. Numbers of individuals in each sample are in parentheses below each site name.

MOLT CYCLE

There are substantial differences in the extent of prenuptial molt in White-crowned Sparrows of the races *nuttalli* and *pugetensis* (Grinnell 1928). Body molt is a complete or nearly complete one in *pugetensis*, the northern race (Banks 1964), but limited in most *nuttalli*, the southern race, to some feathers of the crown and throat (Blanchard 1941). In the populations studied by Blanchard (1941), molt of the central rectrices was confined to populations designated as *pugetensis*. Banks (1964), however, found that more than 13 per cent of his *nuttalli* had replaced both of their central rectrices. His data do indicate, however, that molt of the central rectrices is more common in northern populations.

The intensity of prenuptial molt in our coastal populations is shown in figure 4. Because we found no sex or age differences in the onset, extent, or duration of either the prenuptial or postnuptial molts, all data are combined. Northern populations exhibited a substantially greater amount of molt than southern populations. A relatively steep gradient in intensity of molt is exhibited by the Capetown, Westport, and Albion populations. All birds of the northern populations, with a few exceptions, underwent a heavy prenuptial molt whereas birds of the southern populations usually did not progress beyond the medium molt category if they molted at all (fig. 5). Individual birds from the Westport populations showed considerable variation in their molt, ranging from total absence of molt to the heavy molt designation. The peak of intensity of prenuptial molt occurred progressively later in birds obtained from Bolinas northward to Crescent City. All populations from Crescent City north, with the exception of the Sidney population, exhibited maximum molt on about 11 March. The peak of intensity of prenuptial molt of the Sidney birds occurred on about 4 March.

Blanchard reported that Berkeley *pugetensis* showed the first signs of prenuptial molt on 19 February or later, depending on the year. A few of our captive *pugetensis* and most of those *nuttalli* that went through a normal molt had begun it by 27 January, some three weeks prior to 19 February. On 20 February, 60 per cent of the *pugetensis* had begun their molt (figure 4). Data showing

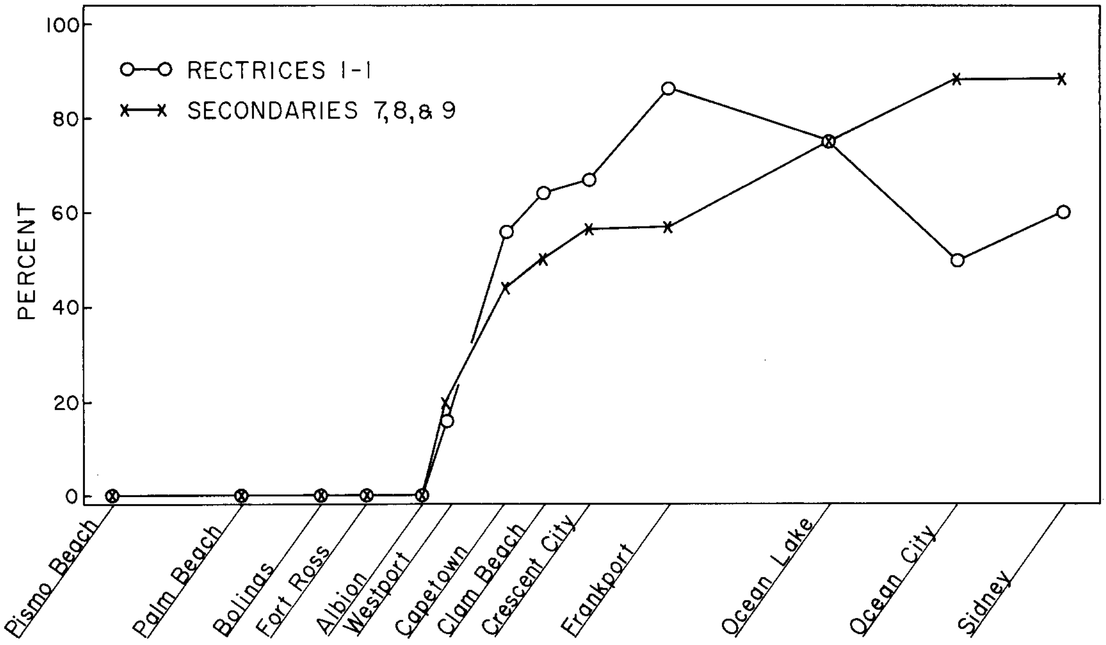

FIGURE 6. Incidence of replacement of rectrices 1–1 and secondaries 7, 8, and 9 in the prenuptial molt of *Zonotrichia leucophrys* from Pacific coastal populations held at San Jose. Relative distances between sites of origin are drawn to scale on the abscissa.

the onset of prenuptial molt in noncaptive *nuttalli* are not available.

At least some individuals of all populations showed prenuptial molt of the crown, body, and coverts. Molt of the central rectrices and secondary remiges occurred in northern populations but was entirely absent in the populations south of Westport (fig. 6). Approximately 20 per cent of the Westport population molted the central rectrices and secondary remiges, compared with 50 to 90 per cent of the birds from populations farther north. In computing these percentages, a bird was considered to be molting the central rectrices if one or both of these feathers were growing, and to be in secondary molt if one or more of the secondaries 7, 8, or 9 were growing. Secondary remiges other than 7, 8, and 9, except in a few cases, were not molted.

The postnuptial molt is complete or nearly complete in all races of the White-crowned Sparrow. Onset of this molt in *nuttalli* in the last week of May was 2 to 3 weeks earlier than its onset in *pugetensis* (fig. 7). All populations progressed through a similar sequence of feather replacement, beginning with the primary remiges and following with the body feathers, rectrices, coverts, and secondary remiges. Crown molt did not begin until 3 to 6 weeks after the initial signs of molt were observed.

GONADAL CYCLE

Comparative testicular cycles of *Z. l. nuttalli* and *Z. l. pugetensis* have been described in

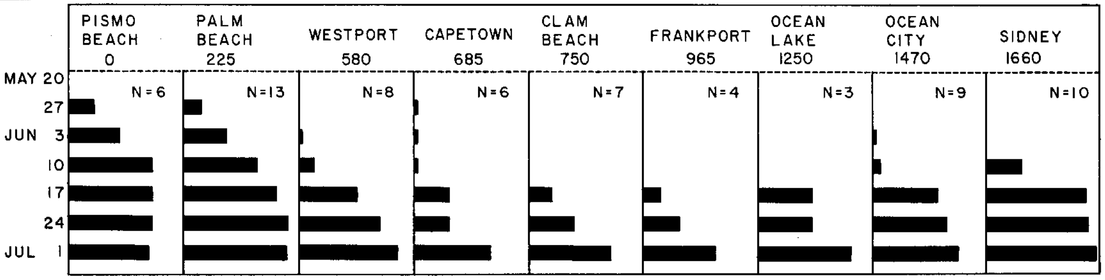

FIGURE 7. Intensity of postnuptial molt at its onset by weeks in White-crowned Sparrows from nine coastal populations held at San Jose in 1960. The longest black bars indicate that nearly all birds were simultaneously in heavy molt in that week. Kilometers north of Pismo Beach are shown below each population site.

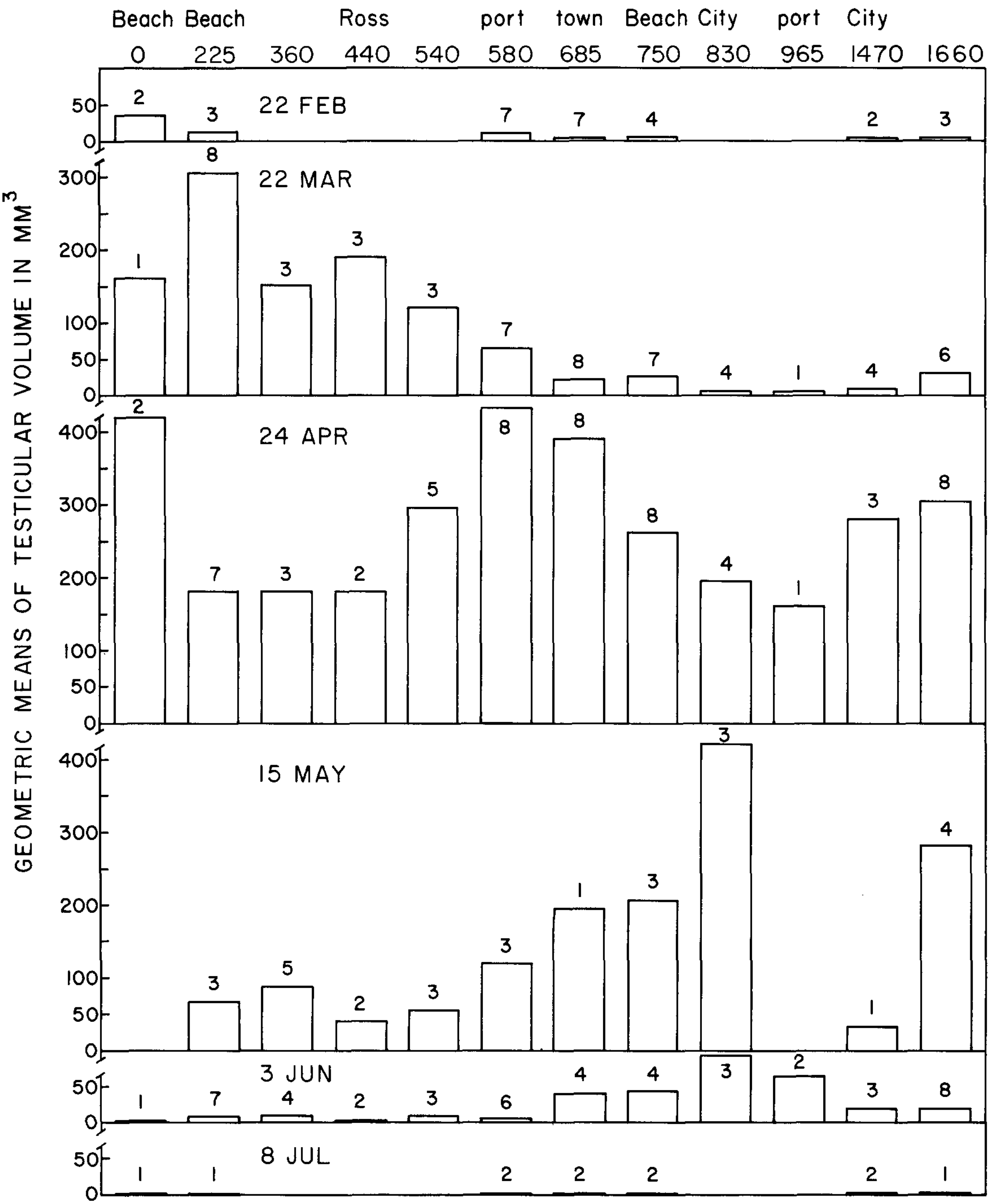

FIGURE 8. Geometric means of testicular volumes of White-crowned Sparrows from 12 Pacific coastal populations held at San Jose on selected dates in 1960 and 1961. Measurements were taken at laparotomy or autopsy. Number of birds is indicated above each bar. Kilometers north of Pismo Beach are shown below each population site.

detail by Blanchard (1941). In the winter and spring following a period of fall inactivity, the testes develop to the breeding condition. Although the testes of both subspecies progress through the same histological stages and reach about the same maximum volume in the spring, Blanchard found that the testes of *nuttalli* develop earlier in the season and at a faster rate than those of *pugetensis*.

In our aviary the birds from the southernmost breeding populations reached the peak of testicular development earliest (fig. 8).

Birds from progressively more northern populations showed peaks of testes development successively later in the season. We found no sharp division between *nuttalli* and *pugetensis* but instead a gradual transition. By making arbitrary groupings, however, we suggest 28 March as the date of the peak of testicular development for birds obtained from the area extending from Pismo Beach to Fort Ross; 28 April for a typical bird from Albion to Clam Beach; and 13 May for a typical Crescent City or Frankport bird. The Ocean City and Sidney populations tended to synchronize with the birds from Albion to Clam Beach.

Our data and those of Blanchard (1941) for wild *pugetensis* and *nuttalli* seem to be in accord when the dates of testicular development are compared; however, the testes of our captive birds regressed several weeks earlier than those of Blanchard's noncaptive birds. The testes of wild *pugetensis* regress in July (Blanchard 1941) and those of wild *nuttalli* in July or August (Mewaldt unpublished data), whereas the testes of our captives regressed in late April to early June soon after peak development was reached. In *Zonotrichia leucophrys gambelii* King *et al.* (1966) observed that testicular regression occurred about two weeks earlier in outdoor captives held in southeastern Washington than in the natural population in Alaska. It is probable that in order for the testes to remain at a high level of development, the birds must actually be breeding. Blanchard's study was based on birds that were observed establishing territories, building nests, and raising young. Our captive birds did not breed, and except for singing and some aggressive behavior by the males they did not show the behavioral characteristics associated with the breeding season.

The testes of birds in some of our captive populations appeared to develop to a greater volume than those of birds of other populations. This difference was in part, if not wholly, a result of performing laparotomies at about monthly intervals and thus by chance at times when the testes were not necessarily at their peak of development. Age differences among birds, as far as could be determined, were not a cause of any difference observed among populations.

Ovarian and follicular dimensions were obtained upon laparotomy of a limited number of female birds. The female does not show sufficient reproductive development under these conditions of captivity to make data analysis fruitful.

ACTIVITY CYCLE

Diurnal activity patterns have been described for several species of *Zonotrichia* (Eyster 1954; Farner, Mewaldt, and King 1954). Activity comes to a peak a few hours after sunrise and then decreases in late morning and early afternoon (Weise 1956). In the evening just before sunset another peak of activity may occur. The morning and evening peaks in *Zonotrichia* are apparently typical of the patterns seen outside the migratory seasons (Mewaldt, Morton, and Brown 1964), and may be an expression of certain intrinsic properties of the circadian clock (Aschoff 1966).

Nocturnal migratory restlessness (*Zugunruhe*) occurs in *Zonotrichia* during the spring and fall beginning at the time when migration ordinarily would take place (Farner, King, and Wilson 1957). Nocturnal locomotor activity is thought to be an expression of the "urge" of caged birds to migrate (Palmgren 1949). Further substantiating this hypothesis, Mewaldt, Morton, and Brown (1964) found that a considerable amount of the nocturnal activity of *Zonotrichia* in circular cages was oriented in the normal direction of migration.

Although nocturnal activity was presumed to be found in migratory forms only (Farner and Mewaldt 1953; Eyster 1954), the nonmigratory *Z. l. nuttalli* have been found to exhibit this phenomenon (Farner, King, and Wilson 1957). Two of four *nuttalli* kept in activity-orientation cages exhibited spring noctural activity when the moon was a prominent feature of the night sky (Smith, Mewaldt, and Brown, unpublished observations). Each, however, showed oriented behavior similar to that exhibited by the migratory races.

The annual cycle of circadian activity patterns of our birds is shown in figure 9. Because only two to four birds from each population were observed and monitored in activity cages and because of considerable individual variability, activity data have been grouped by northern and southern populations. Because three of the four Westport birds resembled the more southern populations in the onset of their spring night activity, the Westport birds are included with the southern populations. All birds captured from Capetown north are included in the northern population.

Experience in our laboratory (Smith, Mewaldt, and Brown, unpublished data) suggests that first-year captive *nuttalli* exhibit more night restlessness than adults from the same flocks. However, because of the mass of data

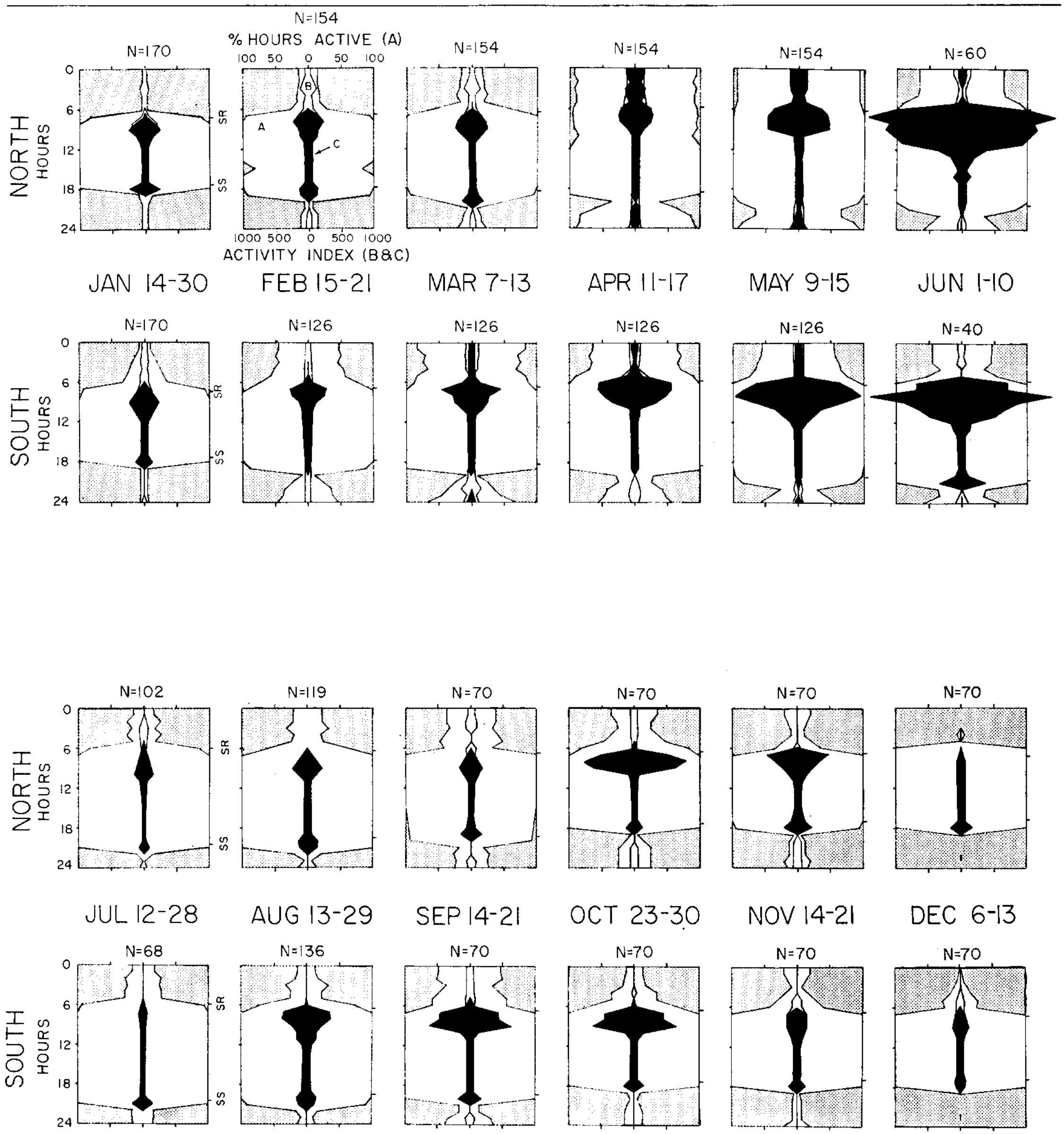

FIGURE 9. Circadian activity patterns of captive northern and southern White-crowned Sparrows in representative periods throughout the year. N = number of bird-days of recording, included 1959–61. SR = sunrise, SS = sunset, A = hourly per cent of birds active, B = median hourly number of perch registrations of only those birds active that hour, and C = median hourly number of perch registrations of all birds present.

accumulated on locomotor activity over the two-year test period, we have found it necessary to combine data for adult and first-year birds as well as data for males and females. These combinations seem justified because we maintained about 70 per cent adults in both the northern and southern test groups and because the 70 to 90 per cent males in the two groups remained comparable from month to month.

Data are presented for representative periods (1 to 2 weeks) of each month of the year. The basic datum is the number of perch registrations per hour. Because numbers of perch registrations per unit time show a positively skewed distribution, we have used the median rather than the mean to describe the intensity of activity. In addition to the median, which includes all hours monitored, we have calculated the active median, which includes only hours with one or more perch registrations. The active median is especially useful because it permits a more realistic inspection of the night component of circadian patterns when only part of a test group is active at night.

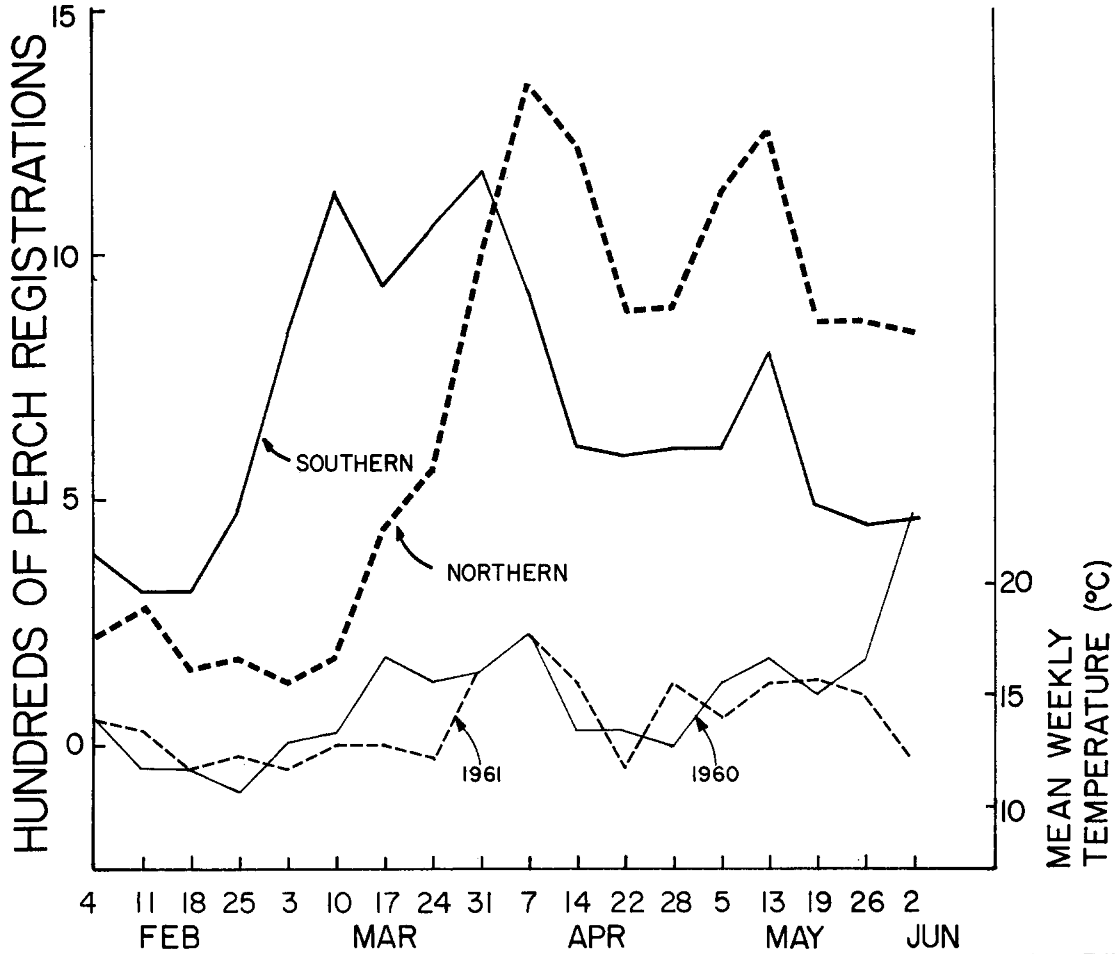

FIGURE 10. Median night locomotor activity (upper curves, scale at left) in spring by weeks (1960 and 1961 combined) for southern and northern Pacific coastal White-crowned Sparrows held at San Jose. Mean weekly temperatures (lower curves, scale at right) are for San Jose.

The per cent of hours during which activity occurred is also shown. During daylight the per cent active hours is, or is nearly, 100. At night each bird was either (1) active at the hour in question each night in the period presented, (2) inactive at that hour each night, or (3) active on some nights only. Most birds behaved consistently, thus falling into categories 1 or 2. When all birds in the population were consistent, the per cent active hours is equal to the per cent of birds showing activity. In some cases, however, when birds were active on some but not all nights, the per cent active hours is lower than the per cent of birds that actually showed some activity. Therefore, the per cent active hours must be interpreted with caution.

The major differences in the annual 24-hour activity pattern between *nuttalli* and *pugetensis* are temporal. A typical *nuttalli* begins to show substantial night activity during the first week of March, whereas night activity of the majority of *pugetensis* is delayed until the last few days of March or the beginning of April (fig. 10), the time when noncaptive *pugetensis* depart from Berkeley (Blanchard 1941) and San Jose. The night activity of *nuttalli* comes to a peak in March compared with the April–May peak of night activity of *pugetensis*. Vernal night activity of *nuttalli* is somewhat sporadic compared with that of *pugetensis*. Seventy-one per cent of the *nuttalli* bird-nights were active from 23:00–24:00 during the March peak compared with 95 per cent of the *pugetensis* bird-nights during May (table 1). A drop in night activity in both *pugetensis* and *nuttalli* in the second half of April is probably due to a drop in temperature at that time in both 1960 and 1961 (fig. 10). The period of at least three months when *nuttalli* and *pugetensis* showed persistent night activity was considerably longer than

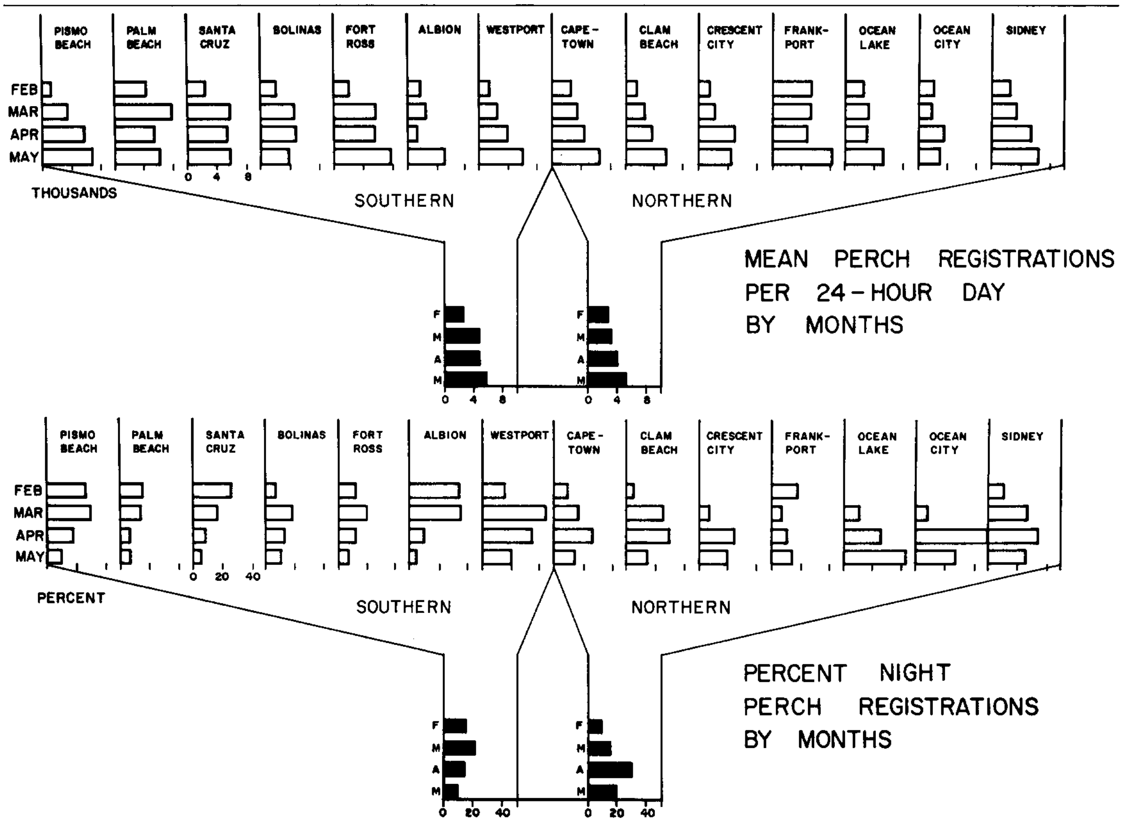

FIGURE 11. Relative quantities of locomotor activity exhibited by seven southern and seven northern populations of Pacific coastal White-crowned Sparrows held at San Jose. The upper figure includes data from all birds for all days in each month in 1960 and 1961. The lower figure shows the per cent of the total locomotor activity that occurred at night. Approximately 4800 bird-days of data are represented in this figure.

the actual period of *pugetensis* migration, which is probably less than a month (Cortopassi and Mewaldt 1965). Extension of *Zugunruhe*, in caged *Zonotrichia*, beyond the actual period of spring migration is apparently characteristic (Mewaldt, Morton, and Brown 1964).

TABLE 1. Per cent of nights that caged Z. *l. pugetensis* and of Z. *l. nuttalli* showed locomotor activity from 23:00–24:00 in selected periods by months in 1960 and 1961. Numerals in parentheses are the numbers of bird-nights tested in each period.

Period	*Z. l. pugetensis*	*Z. l. nuttalli*
14–30 Jan.	4 (100)	6 (95)
15–21 Feb.	14 (134)	45 (106)
7–13 Mar.	22 (153)	71 (122)
4–10 Apr.	82 (152)	62 (124)
2– 8 May	95 (154)	63 (116)
1–10 Jun.	58 (60)	56 (36)
12–28 Jul.	8 (96)	16 (64)
13–29 Aug.	13 (105)	12 (119)
14–21 Sept.	24 (70)	37 (70)
23–30 Oct.	26 (70)	13 (70)
14–21 Nov.	17 (70)	17 (70)
6–13 Dec.	0 (70)	0 (70)

Quantities of total locomotor activity by months for each of the 14 populations increased from February to May (fig. 11). The earlier increase in total activity in four of the seven southern populations in March may well be due to increased daytime locomotor activity associated with readiness to breed and with precocious night restlessness. It is possible that the relative scarcity of prenuptial molt in the southern birds resulted in a favorable energy balance that in captivity was expended in locomotor activity. As might be expected, the percentage of total activity exhibited at night was highest in March in the *nuttalli* and in April in the migratory *pugetensis*.

The occurrence of night activity in our caged *pugetensis* and *nuttalli* was considerably less in fall than in spring. The per cent active hours increased slightly in September for both races (table 1). The patterns of activity during this period were less consistent than during the spring, some birds exhibiting activity on only a few nights of the period shown. The per cent active hours, therefore, is considerably lower than the actual per cent of birds that showed some night activity during the fall. Most birds maintained an evening peak of activity in September in spite of the fact that some of the same birds were active at night. In the spring the evening peak generally disappeared at the onset of night activity.

We suggest that night activity in *nuttalli* is probably an atavistic remnant of an ancestral instinct to migrate. That in *nuttalli* it is a relict of *Zugunruhe* is suggested by its temporal position in relation to testicular development, and by its qualitative and quantitative similarity to *Zugunruhe* in *pugetensis.* We have found that night activity in *nuttalli* is oriented in spring (Smith, Mewaldt, and Brown, unpublished observations). Because many and probably all genes affect several different traits (Mayr 1963), it seems to us to be very likely that such a relict of *Zugunruhe* might persist for some time in a race that has overtly lost the migratory habit. Genetic contact with the migratory *pugetensis* should also favor retention of remnants of *Zugunruhe* in *nuttalli.*

TEMPORAL INTERRELATIONSHIPS AMONG MOLT, TESTICULAR DEVELOPMENT AND ACTIVITY

Molt in *pugetensis* and *nuttalli* is absent or light during the period when the testes are enlarged. *Nuttalli,* which reach the peak of testicular development early, undergo little or no prenuptial molt, whereas *pugetensis* undergo a substantial prenuptial molt before testicular development. In caged *nuttalli* and *pugetensis* the testes regress soon after reaching the peak of development. It is only after regression is well under way that the postnuptial molt begins. *Nuttalli,* as would be expected, begin the molt a few weeks before *pugetensis.* In wild *pugetensis* and *nuttalli* the testes do not regress until July (Blanchard 1941), approximately eight weeks later than in caged birds. The postnuptial molt of both races of noncaptive birds is postponed until August or September.

It is probable that the earlier gonadal hypertrophy of the southern populations results in sex-hormone production that in turn inhibits prenuptial molt. Androgens and estrogens have been shown to suppress the natural molt (Vaugien 1955; Assenmacher 1958). That reproductive activity and molt are usually mutually exclusive has been demonstrated in Red-winged Blackbirds (*Agelaius phoeniceus*) by Wright and Wright (1944) and in White-crowned Sparrows of the race *gambelii* by King *et al.* (1966). The reduction of sex-hormone titer when gonads regress probably contributes to the timing of the start of postnuptial molt. We have recently found several individual wild *nuttalli* at Point Reyes, California, with arrested postnuptial molt in July (unpublished observations). These birds were actively nesting, as indicated by the presence of an incubation patch in females and enlarged cloacal papilla in males. Each bird had new and fully grown right and left first primaries or first and second secondaries, but no other molt was in progress. The early stages of postnuptial molt were probably interrupted by a resurgence of sex hormones associated with another nesting in this multiple-brooded race.

The prenuptial and postnuptial molts in *nuttalli* and *pugetensis* may also be related to total activity level. *Nuttalli,* which underwent little or no prenuptial molt, had a consistently higher level of total activity in the spring than *pugetensis.* This is partly, but not wholly, accounted for by the earlier occurrence and longer persistence of night activity in *nuttalli.* In early summer when the postnuptial molt occurred in our birds there was a sharp decrease in total activity. The reduction in total activity may occur to compensate for the extra amount of energy that has been found to be required by birds in molt (King and Farner 1961).

The major differences between *nuttalli* and *pugetensis* appear to be related to the earlier gonadal development in *nuttalli.* Temporal and quantitative differences in prenuptial molt, postnuptial molt, and activity patterns probably occur either directly or indirectly as a result of the temporal difference in gonadal development.

GENERAL DISCUSSION

Among the observations of Blanchard (1941, 1942) were the following: (1) *pugetensis* that breed at Friday Harbor, Washington, and Comox, British Columbia, have more highly developed testes upon arrival on the breeding grounds than *pugetensis* that breed at Tillamook, Oregon; (2) arrival dates differ only slightly; and (3) the rate of testicular development, at least during early stages, is correlated with the temperature of the environment. Blanchard proposed the following hypothesis: All migratory populations begin migration in the spring at the same physiological threshold that develops in response to similar environmental sequences. *Pugetensis* wintering at the southernmost latitudes begin migration the earliest in the season because of the earlier occurrence of threshold conditions. These birds migrate to the northernmost breeding grounds and therefore presumably spend more time in migration than *pugetensis* that winter farther north and migrate to the southern part of the breeding range. Since considerable testicular development occurs during migration, those *pugetensis* spending the longest time in migration have the most highly developed testes upon arrival at the breeding grounds. Hence *pugetensis* in the northern part of the breeding range (Friday Harbor and Comox) have larger testes upon arrival than *pugetensis* from the southern part (Tillamook).

Data from band recoveries show that *pugetensis* that winter in the San Francisco Bay region of California do in fact breed in the Puget Sound region of Washington and British Columbia at the northern extreme of the breeding range (Cortopassi and Mewaldt 1965). It would be interesting to discover if banded *pugetensis* wintering in northern California would be recovered in the breeding areas in Oregon and southern Washington.

That the testes of all *pugetensis* are at a similar level of development when migration begins is essential in Blanchard's hypothesis. It follows also that the timing of this development is dependent upon temperature and other environmental factors on the wintering grounds. Our data suggest that Blanchard places too much importance on environmental factors in determining interpopulational differences. If Blanchard's hypothesis were correct, the testes of all *pugetensis* housed at San Jose should have begun development on nearly the same date, since the timing of environmental sequences would be the same for all birds. This, however, was not the case. Populations tended to sort out in spite of essentially identical environmental conditions. Generally, *nuttalli* and *pugetensis* from progressively more northern populations showed peaks of testes development successively later in the season. An exception to this trend, however, were the testes of our *pugetensis* from Sidney (probably similar to Blanchard's birds from Comox and Friday Harbor), which reached peak development about the same time or even earlier than testes of *pugetensis* from Crescent City and Frankport (similar to Blanchard's Tillamook birds).

As an alternative hypothesis we propose that interpopulational differences in the date of a specific level of testes development are, for the most part, a result of adaptation to the rainfall and possibly other climatic factors of the breeding grounds. Examination of testicular development dates for individual populations of both *nuttalli* and *pugetensis* (fig. 8) shows a trend toward a later peak of development as latitude, and hence mean annual rainfall, increases. The Sidney area, which is protected by mountains, receives 20 to 30 inches less rainfall per year than adjacent coastal areas (Thomas 1953). As a possible consequence the peak of testes development of our Sidney birds occurred 2 to 3 weeks earlier than would have been predicted from latitude alone. The testes of birds obtained from the Crescent City and Frankport sites appeared to reach the latest peak. Mean annual rainfall from this stretch of coast is high compared with that of other collection sites.

It is logical that the time of gonadal development would be correlated with the climate of the breeding grounds. In an area where climate is less severe, the birds should be able to breed earlier in the season. *Nuttalli,* which breed at the southern latitudes where climate is suitable for breeding relatively early in the season, reach the peak of testes development earlier than *pugetensis,* which breed to the north. An earlier, and hence longer, breeding season in *nuttalli* probably does not result in more fledged offspring since *nuttalli* raise the same number of broods (2 or 3) per year as does *pugetensis* (Blanchard 1941). However, it is probable that among nonmigratory birds (*nuttalli*) those individuals that come into reproductive condition the earliest in the season are able to obtain the most suitable territories.

Our data suggest that the physiological differences among populations are genetic in origin rather than regulated by the environment. Seven of the birds captured in 1959 were held over for the second year of the experiment. Differences in timing of prenuptial molt and *Zugunruhe* between the two years in these birds were small. Data from the second year actually tended to increase the differences among populations rather than decrease them. It is also pertinent that the testicular development of first-year birds, which would not have been able to "set their biological clocks" on the natural wintering grounds, was not appreciably different from that of adults.

Rand (1948), Banks (1964), and Selander (1965) may be consulted for a review of the probable origins of the races of *Zonotrichia leucophrys.* They discuss the several refuges that left pockets of the parent species during the Pleistocene period. Presumably a southwest refuge on the Pacific coast gave rise to the *pugetensis-nuttalli* group. It is further probable that this Pacific coastal group was divided into northern and southern segments during the late Pleistocene to give rise to *pugetensis* and *nuttalli*, respectively.

Grinnell (1928) set the intergradation zone of *nuttalli* and *pugetensis* in Mendocino County in northern California. Blanchard (1942), on the basis of observing the presence or absence of migration, suggested a division point farther north between Eureka (Humboldt County), California, and Tillamook, Oregon. On the basis of our prenuptial molt data, we strongly concur with Banks (1964) who suggested the area between his Humboldt and Mendocino populations as the zone of intergradation. The transition zone of Banks overlaps the northern section of the area suggested by Grinnell, but is clearly to the south of that proposed by Blanchard on the basis of different criteria. Our Westport and Capetown populations, which lie between Banks' Humboldt and Mendocino populations, were clearly intermediate between *nuttalli* and *pugetensis* when the extent of prenuptial molt is considered (figs. 5 and 6). When body weight is considered, a sharp division occurs between Capetown and Clam Beach to the north of Banks' Humboldt populations (fig. 3). The actual zone of transition appears to cover about 100 miles of coastline stretching from the area slightly to the north of Capetown to somewhere in the vicinity of Albion.

Intergradation of two subspecies can be classified as primary if the gradient developed gradually while populations were in continuous contact, or it can be classified as secondary if the two subspecies were at one time separated completely and later came into contact (Mayr 1963). Generally, a smooth transition of characters is indicative of primary intergradation whereas a steep gradient connecting subspecies is characteristic of secondary intergradation.

A rather steep gradient in the Westport-Capetown populations is shown in our data on prenuptial molt and body weight (figs. 3 to 6). Banks (1964) found a similarly steep gradient when he analyzed toe, bill, and tarsal lengths of *nuttalli-pugetensis*. On the basis of these data, intergradation appears to be secondary. The gonadal-cycle data that show a smooth transition would be less suitable for a determination of this type since the temporal differences are probably an adaptation to climate.

The coastline of the Cape Mendocino area where the transition occurs consists of forests and grasslands that extend to the ocean. Habitat there is less suitable for White-crowned Sparrow breeding than most of the other coastal areas, which have considerable chaparral. The apparent scarcity of breeding birds in these forest and grassland habitats suggests a reduced gene flow in the area. It is possible that in the past much more of the coastal area was covered by forests, perhaps enough to isolate completely the breeding ranges of *pugetensis* and *nuttalli*. Successional changes in vegetation in the last several hundred years and, more recently, logging and other activities of man may have gradually reduced the barrier so that *nuttalli* and *pugetensis* are now in contact again.

Salt (1963) proposed the hypothesis that larger species of a genus tend to be those that have occupied their ranges for the shortest time. If his hypothesis is extended to the subspecific level, and if we consider intergradation between *nuttalli* and *pugetensis* to be secondary, birds from the middle of the range should be the largest. This is in fact the situation. Birds from the Bolinas-Fort Ross-Albion segment of coastline have been found both by us and by Banks (1964) to be decidedly larger than those at either extreme of the range. In the areas immediately north of Albion (Westport and Capetown) and immediately south of Bolinas (Santa Cruz) the males in Banks' investigation and the females in our study were clearly intermediate. Our males from these areas were relatively large. Toward the north our males were decidedly large through the Cape Mendocino zone of probable reduced gene flow.

SUMMARY

An assessment was made of certain innate functional attributes of White-crowned Sparrows (*Zonotrichia leucophrys*) obtained from 14 localities in their breeding range in California, Oregon, Washington, and British Columbia. Migratory *Z. l. pugetensis* from extreme northern California to southern British Columbia and nonmigratory *Z. l. nuttalli* from central and southern California were captured on their nesting grounds in June, July, or August. One hundred adults and immatures captured each year (1959 and 1960) in 10 of the 14 localities were studied in outdoor aviaries at San Jose, California. Two birds from each of the 10 localities each year were kept in small cages equipped to monitor locomotor activity continuously. The other birds were kept as a mixed group in large aviaries nearby.

Body weights were higher in winter than in summer, and birds from the middle latitudes were substantially heavier than those from far southern and far northern localities. The migratory form, *pugetensis*, in captivity did not show migratory fat deposition in either spring or fall.

All northern birds down to and including some of the birds from Westport, California, underwent an extensive prenuptial molt. The southern birds began their annual molt three to four weeks earlier than birds from areas north of Westport.

Maximum testicular size was attained in southern birds in March; in birds from the middle latitudes in April; and in northern birds in May. It is hypothesized that hormones associated with the early gonadal growth in southern birds prevented a prenuptial molt.

Nocturnal restlessness occurred in birds from all latitudes. The nonmigratory southern birds showed typical but somewhat less intense night locomotor activity with peaks in March, compared with peak activity in April in northern birds. The existence of night activity in the nonmigratory *nuttalli* can be interpreted as an atavistic remnant of ancestral migratory behavior.

There were distinct differences among the populations in their responses to their common environment at San Jose, including especially differences in the timing of gonadal development, the timing and extent of molt, and the patterns of nocturnal and diurnal locomotor activity. These differences are genetic in origin.

The data suggest that the area of steepest variation and reduced gene flow between *pugetensis* and *nuttalli* is between Capetown and Westport on the north coast of California.

ACKNOWLEDGMENTS

We are especially grateful to Irene L. Brown who participated extensively in the planning, execution, and interpretation of this investigation. We acknowledge the assistance of many students, colleagues, and landowners who contributed in the capture, transport, and care of the birds and in the painstaking analysis of nearly 200,000 bird hours of locomotor activity data. These include Lester Brubaker, Laura Erickson, Frances Mewaldt, William Mewaldt, Herbert Royse, Robert W. Smith, Doris Tengan, and Mildred Tomooka.

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Accepted for publication 22 September 1967.