SEASONAL SEX AND AGE RATIOS IN POPULATIONS OF THE WHITE-CROWNED SPARROWS OF THE RACE *GAMBELII*

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The existence of geographic and temporal segregation of the sexes and age classes during the migration of birds has been an accepted concept for many years. For relatively few species, however, are the data adequate to demonstrate convincingly that there are differences with respect to age or sex in the schedule of migration, in the routes of migration, or in wintering populations (Eaton, 1933; Frieling, 1934; Nice, 1937; Thomson, 1939; van Dobben and Mörzer Bruyns, 1939; Lack, 1943, 1944; Deelder, 1949; Bellrose, Scott, Hawkins, and Low, 1961; Jehl, 1963; Schifferli, 1963). The available data are not sufficient to reveal common or consistent patterns of differential migration in any group of birds, if, indeed, such patterns exist. The evolution of this opinion has been ably reviewed by Tordoff and Mengel (1956), and the history of the subject need not be reiterated here. We believe that a rigorous analysis of patterns of differential migration must be based on a larger fund of comparative data than is currently available. The present report is intended in part as a contribution to this fund based on data on the White-crowned Sparrow of the race *Zonotrichia leucophrys gambelii.*

It should be emphasized also that differential migration has a general relevance to many types of investigations in avian biology, quite apart from its basic relationship to problems of population dynamics. The existence of differential timing, routes, and destinations in the migration of different components of a population has an obvious bearing, for instance, on investigations of population genetics, speciation, homing and navigation, and physiological ecology. Thus, intensive study of differential migration is especially pertinent in taxa such as *Zonotrichia* that have been widely used in investigations in avian biology.

MATERIAL AND METHODS

Collection sites.—Samples of *Zonotrichia leucophrys gambelii* were obtained annually from 1952 through 1964 from migrating flocks near Pullman, Whitman County, Washington, in April and May and in September and October. Samples of winter-resident populations were collected in western central California (Santa Clara, Santa Cruz, and Alameda counties) and along the Snake River Canyon about 30 kilometers south of Pullman. The former area is approximately at the middle of the latitudinal range of *Z. l. gambelii* in winter; the latter is at the extreme northern

margin of the winter range of the species in the intermountain region. Samples of *gambelii* from the breeding area were obtained during July and August, 1962, near Fairbanks, Alaska. We do not know whether the populations sampled in California and in Washington were derived from the breeding population of central Alaska or from elsewhere.

Collection methods.—Winter-resident populations in California were taken in mist nets. We have no reason to believe that the age and sex classes have a differential susceptibility to capture by this method when the birds are in mixed flocks during the nonbreeding seasons. We therefore assume that collections are random samples of the populations at the stated times and places.

In the breeding area, White-crowned Sparrows were collected by shooting or by capture in mist nets. Each of these methods is subject to a characteristic bias associated with the behavior of the birds during different phases of the annual cycle. These potential sources of error will be discussed subsequently. Adult and immature birds were distinguished by differences in the coloration of the crown. Sex was determined by laparotomy or by post-mortem dissection.

Statistical analysis.—For analysis we have pooled the data by months for the period of winter residence and, in order to reveal population flux more accurately, by ten-day intervals during the postnuptial period and during the periods in migration in southeastern Washington. The timing of collection periods in California prohibits a useful analysis of these data in terms of population flux during migration. In analyzing the data, the confidence levels for differences among ratios were computed from the chi-square distribution, with the addition of the Yates correction for continuity where applicable. The 95 per cent confidence interval was estimated from the relation, $S_r t$, where t = "Student's t," and $S_r = (pq/N)^{1/2}$, in which p = percentage male or percentage adult, q = 100 − p, and N = sample size.

RESULTS AND DISCUSSION

POSTNUPTIAL SEASON IN ALASKA

The reliability of the subsequent interpretations of changes in the composition of migrant and of overwintering populations of White-crowned Sparrows depends in part on an accurate estimate of the composition of the population at the end of the reproductive period. Unfortunately, it is during this season that the behavior of adult males and adult females and of adults and immatures differs most conspicuously and thus introduces bias into the sampling methods. Although a thorough knowledge of the sequence of behavioral changes in the birds during the postnuptial period enables us to select data obtained by methods and at times that are most likely to yield random samples, the conclusions that can be supported by these data are clearly provisional.

The data in table 1 were obtained after the end of the fledging period, about July 10, in 1961. By this time, the males had practically ceased to sing, family groups of juveniles were coalescing into small flocks, and there were no discernible differences in the behavior of adult males and females.

Sex ratios.—In July, all adults taken in nets were retained as specimens; likewise, birds taken by shooting were not intentionally selected for sex. In neither type of collection in July does the sex ratio differ significantly from unity. This is in accord with our field observations that there were essentially no unmated birds in several intensely studied nesting populations near Fairbanks, and with the sex ratio of adults (51.0 per cent males; N = 343) in the total sample of autumn migrants taken

TABLE 1

COMPOSITION OF SAMPLES OF *Zonotrichia leucophrys gambelii* TAKEN
NEAR FAIRBANKS, ALASKA, DURING THE POSTNUPTIAL PERIOD

Class (no. and per cent)	July 6–31			August 1–29		
	Net	Shot	Both	Net	Shot	Both
Adult male,	18	23	41	23	18	41
female,	17	23	40	17	7	24
both,	36[a]	47[a]	83[a]	42[a]	25	67[a]
per cent male	51	50	—	57	72	—
Im. male,	15	6	21	34	7	41
female,	11	5	16	13	4	1⁻
both,	133	11	144	129	11	140
per cent male	58	54	—	72	64	—
Total birds,	169	58	227	171	36	207
per cent im.	79	—	—	75	—	—

a Includes birds of unknown sex.

at Pullman. However, for reasons that will be discussed subsequently, it may not be acceptable to construe the latter as supporting evidence.

After about August 1, it became desirable to collect principally males, with the results shown also in table 1. During this period, the larger, relatively long-tailed birds were selected from the netted samples, and adults that "looked" like males were selected in collection by shotgun. The bias in collection yielded samples that were weighted in favor of males, although the sex ratio was not significantly ($0.5 < P < 0.3$) different than unity in the case of the net-caught sample.

In the case of immature birds, the collections were not intentionally biased in July, and the ratios do not differ significantly from unity, although apparently they are weighted slightly toward males. In August, with intentional bias toward males, the sex ratio was significantly ($P = 0.05$) weighted in the net-caught sample, but not in the small sample collected by shooting.

Although there is no reason a priori to assume a balanced sex ratio in adults of even monogamous species of birds (Mayr, 1939), we believe that our data support the conclusion that there are practically equal numbers of males and females in the population near Fairbanks during the postnuptial period. Although the increase in the proportion of males in the samples in August might reflect a differential mortality affecting mainly females, it is more probable that this increase resulted from the intentional sample bias described in the preceding paragraphs.

Age ratios.—The data were not exposed to human bias in the classification of age groups. All captured birds were classified. Nevertheless, there are marked differences in the behavior of adult and immature birds in late summer that potentially distort the samples and make estimation of the true proportions of the age classes in the total population very difficult. The data in figure 1 clearly reflect the following sequence of events. During the first 10 days of July in 1961, the fledging period was terminating in the majority of pairs and there were many family groups of essentially independent immature birds accompanied by the adults. During this period, the proportion of immature birds in the samples lay between 70 per cent and 80 per cent, resembling the ratios found during the autumn migration at Pullman (fig. 4). During mid-July, immature birds began to gather into large flocks; these became especially conspicuous in late July and thereafter. The adult birds, unlike the immatures,
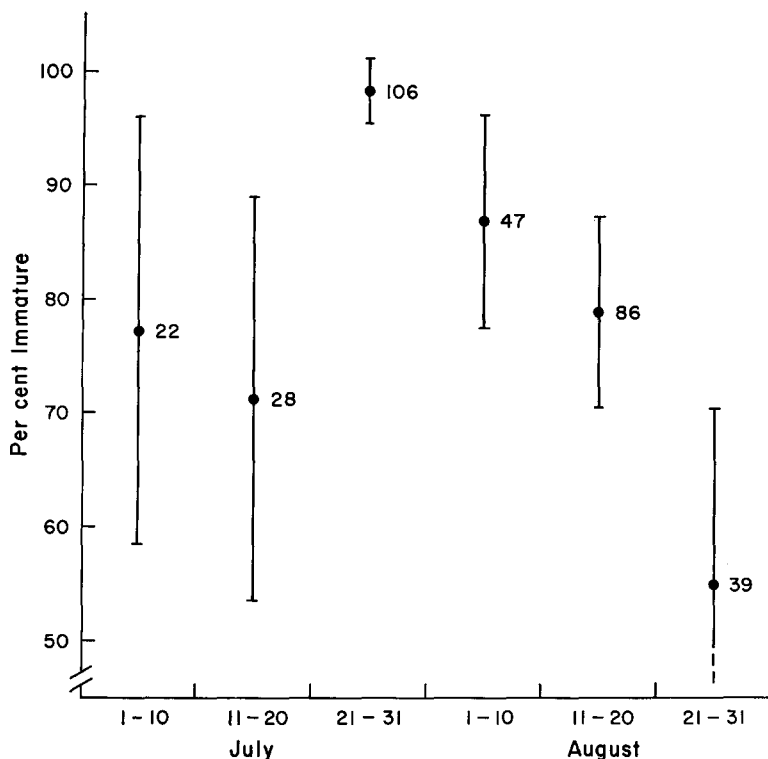
Fig. 1. Age composition of populations of *Zonotrichia leucophrys gambelii* sampled by capture in mist nets during the postnuptial season in central Alaska. Points indicate mean values; vertical bars depict the 95 per cent confidence intervals. Numerals at each point denote sample size.

retained some degree of territorialism and joined the vagrant flocks of immatures only gradually during the late stages of the postnuptial molt in mid-August. During this period, the composition of the samples decreased from essentially 100 per cent immature birds toward the level of 70–80 per cent immatures. With the beginning of the migratory season in late August, the proportion of immature birds continued to decline below its previous minimum level. Possibly this was the result of dilution of the local population by the arrival of early adult migrants from the north, but it is perhaps more probable that it was caused entirely or in part by an earlier departure of some of the immature birds from the local population.

We recognize, but cannot assess, the potential role of differential mortality in influencing the observed variation in age-composition of the population. If this factor may be disregarded in initial approximations, then we estimate that the population of White-crowned Sparrows in central Alaska during the immediate postnuptial season should contain about 60 per cent to 70 per cent immature birds. Our data for two seasons indicate that the average clutch near Fairbanks contains 4.92 eggs (256 eggs in 52 nests), and that hatching success is about 95 per cent (in a sample of 130 eggs, 6 were infertile or addled, none was lost to predators or abandonment of the nest). If the nestlings from these eggs were all successfully fledged, then the proportion of

immature birds in the population, assuming a balanced sex ratio in adults, would be 70 per cent. We have no information on fledging success in the population of White-crowned Sparrows near Fairbanks. The limited data of Oakeson (1954) suggest a minimum fledging success of 75 per cent during one season near Mountain Village, Alaska. Although we know of no other adequate data on the fledging success of ground-nesting altricial birds in the Arctic, it seems reasonable that it will be of a high order, lying within or exceeding the upper range of success (60 per cent to 70 per cent) found in similar species of the North Temperate Zone (Nice, 1957). Certainly the highly favorable average weather conditions in central Alaska during late May, June, and July, combined with the low density of nest predators, would favor the survival of nestlings.

On the basis of a hypothetical fledging success of 75 per cent, the population of White-crowned Sparrows at Fairbanks would contain 64 per cent immature birds. The actual proportions were 71 per cent to 74 per cent in samples taken by net in July, before the segregation of the immatures into summer flocks (fig. 1). The discrepancy between these data and the estimated proportions of 64 per cent to 70 per cent (assuming fledging successes of 75 per cent and 100 per cent, respectively) might be due to differential rates of mortality, or to bias in sampling, or both. However, since the rate of mortality is usually highest during the first year of life among passerines (Farner, 1955), it is probable that bias in sampling was the predominant factor; that is, that adults were slightly more difficult to catch during the postnuptial season.

AUTUMN MIGRATION

The autumn passage of White-crowned Sparrows through southeastern Washington usually begins during the first week of September and terminates with a few stragglers soon after mid-October. The large majority of the population passes during the interval from September 10 to September 30. Birds netted in the uplands until October 10 are regarded as migrants; birds caught in the Snake River Canyon after October 31 are regarded as winter residents.

Sex ratios.—We proceed from the assumption that the sex ratio in the postnuptial population does not deviate greatly from unity in either adult or immature birds. The averaged data on sex ratio for the period from 1952 to 1964 are shown in figure 2. The regular increase in the proportion of males in the migrant population during September and early October makes it clear that there is a distinct differential migration of the sexes. In individual years for which there are sufficient data, this pattern of change is also revealed, resembling closely that found by Millar (MS, Univ. Wisconsin) in the White-throated Sparrow (*Zonotrichia albicollis*) in Wisconsin. The obvious interpretation of these data is that they reflect a temporal differentiation of migratory schedule in the two sexes, the males lagging behind the females. However, it is an equally plausible hypothesis that the data may reflect a geographic rather than temporal differentiation in the migratory itinerary of the two sexes. Assuming this alternative, consider the following hypothetical situation:

Population S occupies a breeding area mostly south of population N. In each population the postnuptial sex ratio is 50 per cent males, but in each there is a geographic segregation of the sexes over two or more southbound routes during autumn migration, so that the sex ratios in the subpopulations following each route differ from unity. Suppose that one route from each population converges on a common route, and that at Pullman we sample the randomly mingled subpopulations derived from N and S (fig. 3A). In conformance with the assumption that we deal only with geographic segregation of the sexes, suppose further that the sex ratios of the subpopula-
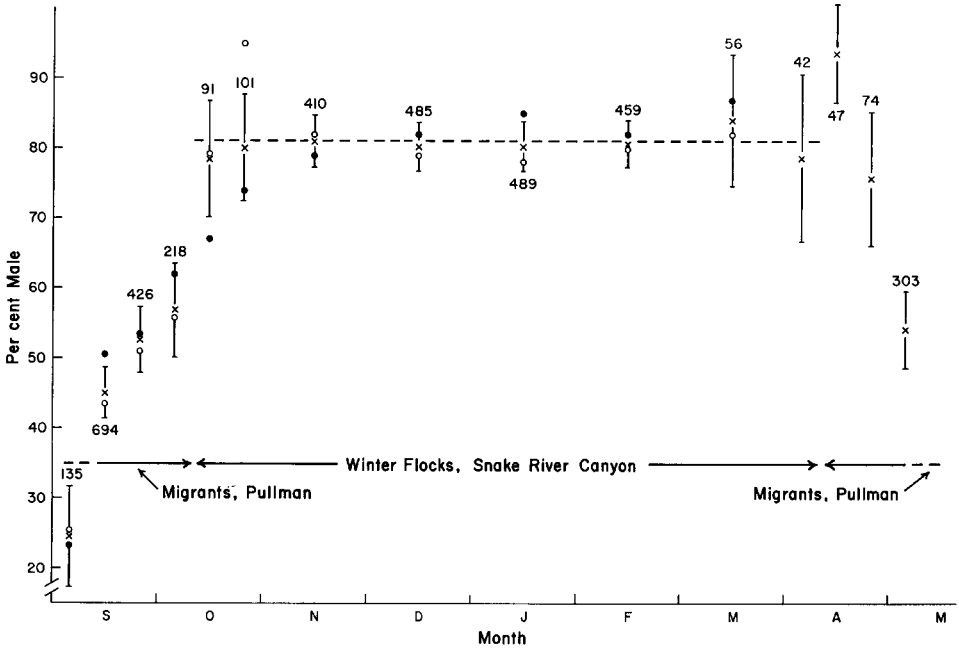
Fig. 2. Sex composition of populations of *Zonotrichia leucophrys gambelii* sampled by capture in mist nets in southeastern Washington. Filled circles and open circles indicate mean values for adults and immatures, respectively; crosses indicate mean values for the combined age classes. Vertical bars depict the 95 per cent confidence intervals for the combined data; numerals at each point denote sample size, ages combined. The horizontal broken line indicates the mean value for the combined winter samples.

tions are stable but different from one another. Finally, assume that the elements of the southern population arrive first at the sampling station and that the elements of the northern population arrive later, but in time to overlap the passage of the first subpopulation. The fractions of the parent populations will thus vary between zero and unity in the derivative population. It follows that the fraction of males (f ♂) in the derivative population will be the ratio of the sum of males from each parent population to the total number of birds in the sample,

$$f ♂ = \frac{Np + Sq}{N + S} \qquad (1)$$

where $N =$ the numbers of birds from population N in the sample, $S =$ the number of birds from population S, and p and q are, respectively, the fractions of males in the subpopulations.

Equation 1 may be simplified as follows:

$$f ♂ = \frac{Np}{N + S} + \frac{Sq}{N + S} = np + sq \qquad (2)$$

where n and s are the respective fractions of the parent populations in the sampled population. And, since $s = 1 - n$,

$$\begin{aligned} f ♂ &= np + (1 - n)q \\ &= n(p - q) + q = s(q - p) + p \end{aligned} \qquad (3)$$

Because p and q are constants under the conditions stated, it is obvious from equation 3 that the sex ratio of the sample, f ♂, is a function only of the proportions of the parent populations in the sampled population. If these populations converge at a constant rate, then the change in sex
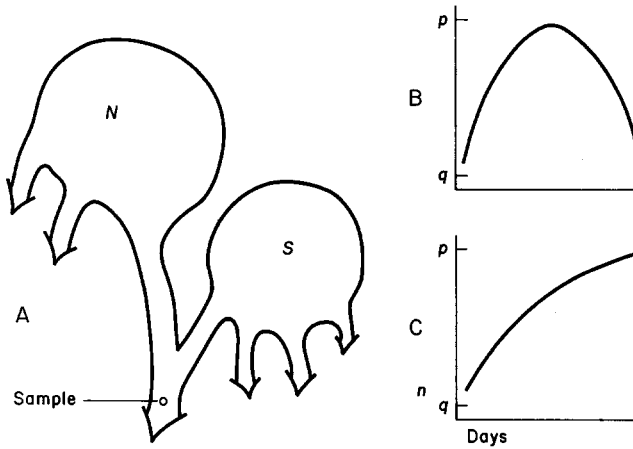
Fig. 3. Hypothetical model of temporal variation in the composition of a subpopulation derived from merging elements of two parent populations. See text for discussion.

ratio in the sampled population will be a linear function of time, varying within the numerical limits of p and q. If the rate of convergence of the parent subpopulations is nonuniform, then n as a function of time can assume an essentially infinite variety of forms depending on the differential rates of passage of the components of the parent populations. These ramifications cannot be usefully explored in the present report. It may be noted, however, that only two general modes of change are possible within the structure of the model. If the elements of the parent populations pass through the sampling station on exactly the same time schedule, even though in varying proportions within this schedule, then the value of n, and hence of f♂, will pass through a value (minimum or maximum) lying between p and q. An example is shown schematically in figure 3B. However, if the schedules of passage are not simultaneous, then n will approach p as a limiting value (minimum or maximum) if N is the later component, or will approach q if S is the later component. One form of this situation is shown schematically in figure 3C. Obviously, the form of n (and hence of f♂) as a function of time will be determined by the congruence of the time-distribution curves of N and S in the sampled population. Nevertheless, the empirical data (fig. 2) showing the change in sex ratio during autumn migration conform in type to the system depicted in figure 3C, opening the possibility that at Pullman we may be sampling the merged elements of two migrating populations in which the proportion of males in the first element to arrive is smaller than the proportion in the later element.

Finally, it is evident that the observed change in sex ratio during autumn migration may be a compound result of both temporal and geographic differentiation in the migratory habits of the sexes. While it remains clear that a sexual differentiation in itinerary does exist, it is impossible to identify with certainty the components of this differentiation by the use of samples obtained at only a single point on the migration routes. Although this interpretation of our data may be regarded as hypercautious, we believe that it is the only one tenable in view of our ignorance of the extent of a geographic differentiation in the migration of the two sexes. Stack and Harned (1944), Fischer and Gill (1946), and Ishizawa (1963) comment on the complexity and apparent variability of the itinerary of migration in songbirds.

Age ratios.—The change in the proportions of adult and of immature White-crowned Sparrows in migrating flocks in southeastern Washington shows no clear consistency from year to year except for a tendency toward an increase in the pro-

TABLE 2

EXAMPLES OF ANNUAL DIFFERENCES IN THE AGE COMPOSITION OF
MIGRANT FLOCKS OF *Zonotrichia leucophrys gambelii*

Period	1958 No.	1958 Per cent im.	1961 No.	1961 Per cent im.	1963 No.	1963 Per cent im.	1964 No.	1964 Per cent im.
Sept. 1–10	28	75	136	97	—	—	316	84
Sept. 11–20	169	69	231	84	361	69	697	86
Sept. 21–30	45	53	—	—	144	73	80	93
Oct. 1–10	18	83	8	87	115	93	—	—

portion of immatures in the late stages of migration. In individual years for which we have samples of useful size, the earliest migrants may be almost entirely immatures, as in 1961 (table 2), tending then to decrease in the middle samples; or the early flocks may contain a proportion of immatures close to the long-term mean, tending then to decline until late September (for example, 1958), to remain stable (for example, 1961), or to increase (for example, 1964). On the average, the migrant flocks contain about 80 per cent immature birds in September (fig. 4). The average for the period of migration (September 1–October 10) is 79.4 per cent immatures (N = 3032). This exceeds significantly the value given by Drost (1935) for *Fringilla c. coelebs* (72 per cent immatures), *Phoenicurus phoenicurus* (61 per cent immatures), and *Turdus merula* (63 per cent immatures) during autumn migration in central Europe. The discrepancies may result, of course, from differences in rates of reproduction, in population dynamics during migration, or both.

In samples of migrant White-crowned Sparrows in southeastern Washington taken in late September or early October there was a significant increase (P < 0.01) in the fraction of immature birds to about 85 per cent. There were no statistically significant differences in sex ratios in the two age classes at any time, indicating that the sexes tend to act similarly at this season regardless of age. Superficially, the increase in the proportion of immature birds in samples taken at the termination of migration can be interpreted to indicate that, on the average over a period of several years, the young birds tend to migrate more slowly than adults, or to leave the breeding area later although moving at the same speed, or to leave earlier but to migrate much more slowly. However, our data cannot exclude the possibility that the change in age ratio at Pullman actually reflects a more complex situation of the type described in the preceding section. It seems clear that there is a minor tendency toward differentiation in the migratory itineraries of adults and immatures, but we cannot identify the relative importance of temporal and of geographic components. Borror (1948), in a sample of 387 *Zonotrichia albicollis* obtained during 6 migratory periods in Michigan, did not detect any significant changes in age ratio during autumn migration. Immatures apparently comprised, on the average, 31.2 per cent of the population during these periods. However, as the author notes, age-determination on the basis of plumage characteristics may not be an entirely reliable method in *Z. albicollis* (see Wolfson, 1954).

Nisbit *et al.* (1963) present data showing that there are no significant temporal changes in the proportions of the age or sex classes in samples of *Dendroica striata* taken during autumn migration in New England. Drury and Keith (1962) show that there is a relatively large proportion of immature *Dendroica striata* in samples obtained along the New England coast, and a relatively small percentage of immatures in samples obtained at inland stations. Taken together, these data suggest that
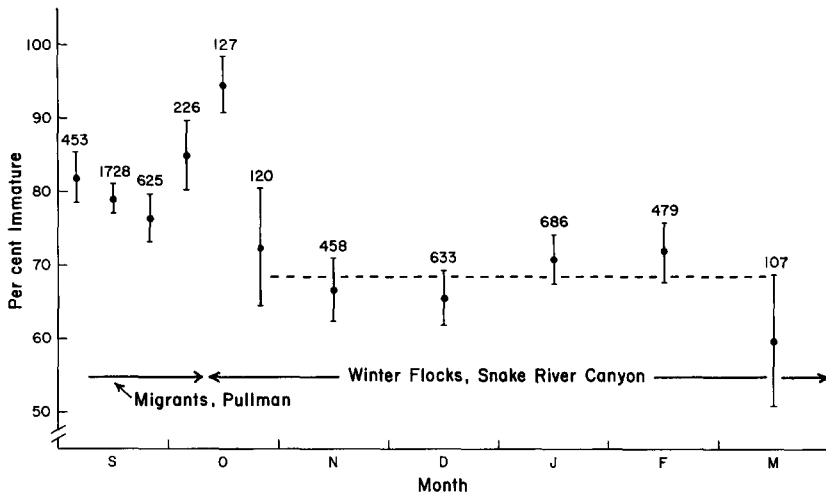
Fig. 4. Age composition of populations of *Zonotrichia leucophrys gambelii* sampled by cap-
ture in mist nets in southeastern Washington. Points denote mean values; vertical bars
depict the 95 per cent confidence intervals. Numerals at each point denote sample size.
The data for the sexes are combined. The horizontal broken line indicates the mean value
for the combined winter samples.

Dendroica striata may display a predominantly geographic difference in the migratory
itineraries of the age classes.

The extensive observations of Dobrynin (1963) on the fall migration of *Fringilla
coelebs* at Kurisch Bay on the Baltic Sea in 1962 strongly suggest four waves of first-
year birds and two maxima in movement of females, indicating the possibility of a
temporal succession of populations in migration.

WINTER RESIDENT POPULATIONS

The migration of White-crowned Sparrows in southeastern Washington essentially
terminates in mid-October, although a few stragglers can be found later in October.
Late October is therefore a period of declining migratory flux and of stabilization of
the winter population at the northern margin of the winter range. From November
through March, field observations give the impression that the local population in
the Snake River Canyon is stable and sedentary. We find that White-crowned Spar-
rows form localized, discrete winter flocks (see Blanchard and Erickson, 1949) among
which there is little if any interchange. Furthermore, areas of the Snake River Can-
yon from which flocks have been removed by capture remain empty for the remainder
of the winter, suggesting that there is negligible population movement during this
time. Pressures causing local movements seem to be absent from this canyon-bottom
situation in which the distribution of the flocks is linear. Suitable habitat is discon-
tinuous, and the Snake River itself tends to be an effective barrier to flock movement.
In central California, however, with a much greater density of wintering *Z. l. gam-
belii, Z. l. pugetensis* (Cortopassi and Mewaldt, 1965), and *Z. atricapilla,* wintering
flocks are scattered over broad areas, and tend to be in contact with other flocks on
all sides. In this situation, flock ranges appear to be more plastic and interchanges
of individuals more frequent (Mewaldt, 1964).

TABLE 3

VARIATION BY SITE IN THE AGE RATIO IN SAMPLES OF *Zonotrichia*
leucophrys gambelii CAPTURED IN THE SNAKE RIVER CANYON

Area[a]	No.	Per cent Im.
0–5 km.	634	73.3
5–13	676	71.0
13–16	308	56.8
19–23	230	63.0
35–42	513	78.0

[a] Kilometer 0 = Wawawai, Whitman County,
Washington; distance measured upstream (southwest).

Our netting stations in the Snake River Canyon were scattered at irregular inter-
vals over a distance of about 48 kilometers upstream from Wawawai, Washington.
Analysis of our data in terms of site of capture reveals that the sex ratio was essen-
tially uniform throughout the sampling area, but that, during the period of this inves-
tigation, there was a nonuniform distribution of age classes (table 3). We find no
obvious correlation of this pattern with local topography, ecological conditions, or
climate. Sampling stations in California, in contrast, were widely scattered in a mosaic
pattern in which we do not find a geographic segregation of classes.

Sex ratios.—Data displayed in figure 2 show that the sex composition of the
population in southeastern Washington was stable at about 80 per cent males from
mid-October through March (Mewaldt and Farner, 1953). There were no significant
differences of sex ratio in the two age classes. If we accept the conclusion that the
postnuptial sex ratio is unity in adults and immatures, then it becomes evident that
there is a geographic differentiation in the wintering areas of the sexes, the females
tending to overwinter farther south. Our data from central California indicate that
the winter populations consisted of about 64 per cent males (N = 552). The latter
samples were biased by an attempted selection for males in about one-third of the
collections. In spite of this, the data demonstrate that males were less abundant in
central California (less than 64 per cent of the population) than they were in south-
eastern Washington (80 per cent).

In an effort to reveal more fully the patterns of sexual segregation, we have exam-
ined data obtained from museum specimens of *Z. l. gambelii* collected during the
period of winter residence. These data, together with those of Hardy, Roberts, and
Banks (1965), are displayed in figure 5. Because the samples are few, are often
numerically small, and may be biased by unsuspected factors, interpretations can
be only provisional. Nevertheless, the data appear to reveal patterns of geographic
segregation of the sexes in *Z. l. gambelii* that deserve additional investigation. There
are apparent decreases in the proportion of males in the populations southward along
the Pacific Coast, through the Central Valley of California, and through the Great
Basin into Sonora and Sinaloa. Statistical comparisons of the sex ratios in these sam-
ples show that they all contain a significantly smaller (P < 0.01) proportion of males
than do the populations in southeastern Washington. Along the Pacific Coast, al-
though the trend seems clear, the difference between the ratio in middle California
and in Baja California is of only marginal significance (0.1 < P < 0.2). In the Cen-
tral Valley of California, a sample obtained from the entire valley contained a greater
proportion of males (66 per cent) than a sample from the extreme southern end of
the valley (50 per cent; Hardy, Roberts, and Banks, 1965). The difference is statisti-
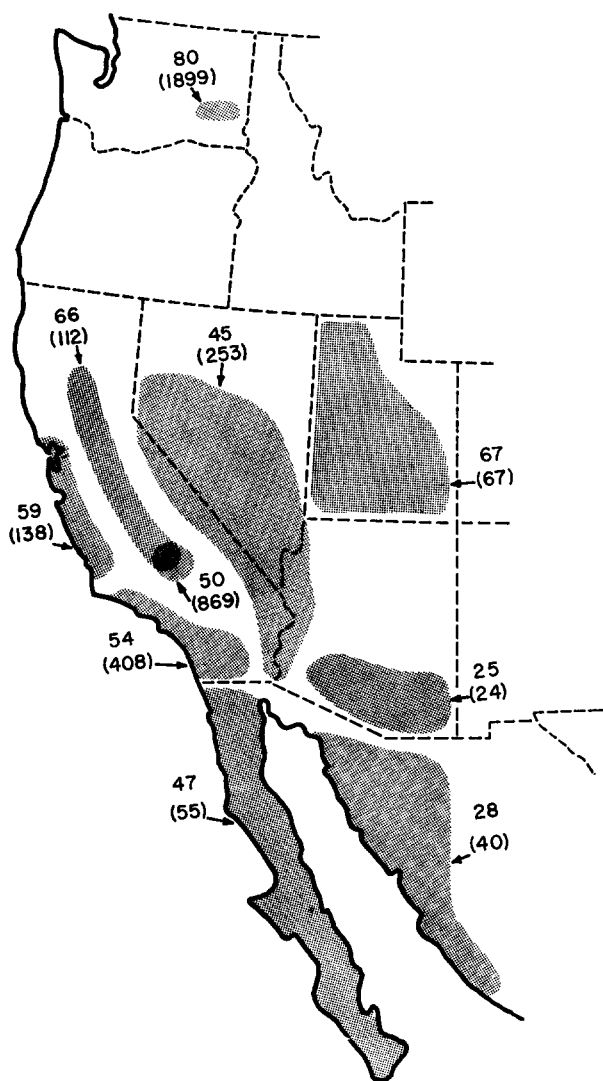
Fig. 5. Geographic variation of sex composition in museum collections and net-caught samples (southeastern Washington and southern San Joaquin Valley) of *Zonotrichia leucophrys gambelii* during the period of winter residence. Numerals in parentheses indicate sample size; numerals without parentheses denote percentage males in the samples obtained within the stippled areas.

cally significant (P < 0.01). It is noteworthy also that Emlen (1943) reported that a sample of 181 *Z. l. gambelii* taken in the Central Valley near Davis, slightly north of the latitude of San Francisco, contained 79 per cent males. Considered together, these data suggest a north-south segregation of sexes in the Central Valley, as along the coast. A similar situation appears to exist east of the Sierra Nevada through the Great Basin into northwestern México. The sample from Nevada, eastern California, and western Arizona contained a significantly greater (P < 0.01) proportion of males

(45 per cent) than collections from south-central Arizona (25 per cent) and Sonora and Sinaloa (28 per cent). The sex ratio as a function of latitude appears to decrease more rapidly southward in these populations than in those sampled in western California; that is, the males apparently tend to remain farther north in winter. However, it is equally plausible, as Emlen (1943) concluded previously from similar data, that the samples may reflect a partial longitudinal segregation of the sexes, the males going predominantly west of the Sierra Nevada. The pattern of latitudinal sexual segregation in *Z. l. gambelii* appears to be similar to that found in the Chaffinch, *Fringilla coelebs* (Schifferli, 1963), in Russian populations of the Snow Bunting, *Plectrophenax nivalis* (Larionov, 1927), and in the sapsuckers, *Sphyrapicus* (Howell, 1953; Davis, 1962). The tendency of males of these species to winter at higher latitudes may be an adaptation that favors their earlier arrival in the breeding areas (see Tinbergen, 1939; Howell, 1953; Oakeson, 1954; Irving, 1960), and in turn it assures an orderly establishment of territories before the arrival of females.

The significance of the large fraction of males in the samples from Utah is uncertain. A priori, the separation of samples from Utah from those obtained in the more western parts of the same biotic region is not logically defensible; yet, the existence of a highly significant difference (P < 0.001) between the two groups implies that the composition of the wintering populations is not uniform throughout the region.

Age ratios.—At the termination of autumn migration and at the time in which winter flocks are forming there is evidently still some flux in the population in the Snake River Canyon (fig. 4). In the interval from October 11 to October 31 there was a significant (P < 0.01) decrease in the immature fraction from about 95 per cent to about 72 per cent. There are no statistically significant differences between the sexes during this period. This change may result from a differential mortality, or from a late departure of immature birds that have lingered in the Snake River Canyon, or from the addition of late-arriving adults. Because of the increased influx of immature birds during the late stages of migration (fig. 4) we believe that the second alternative is the more probable.

From November through February the age composition of the winter flocks in the Snake River Canyon was relatively stable, although showing an apparent increase from about 65 per cent immatures to about 75 per cent immatures. The difference between the means for November and February is of only marginal statistical significance (0.1 < P < 0.05), and probably results from bias of the samples. We have already mentioned that during the period of this investigation there was a geographic variation of age ratio within the population in the Snake River Canyon (table 3). By chance, the temporal distribution of sampling emphasized areas with lower proportions of immature birds early in the winter, while areas with greater proportions of immature birds were used more heavily late in the winter. This produced the apparent trend shown in figure 4, which could be rationalized otherwise only by the unlikely possibility of a differential mortality acting against adult birds or by a minor population flux continuing through the winter. The apparent decrease in the fraction of immature birds in March (fig. 4) accompanied the prenuptial molt, and reflected the change of crown pattern to the adult form. After the end of March, all birds were in adult plumage.

In the combined samples from all stations in the Snake River Canyon, the population consisted of 68.8 per cent immature birds (N = 2256) during the period from November through February. In central California, the mean age composition of the

winter population varied from 63 per cent immatures in November, to 57 per cent in December, 58 per cent in January, and 60 per cent in February. The decrease in the fraction of immatures between November and December is statistically significant (P < 0.01; N = 1557), but thereafter the age composition of the population was apparently stable. The fraction of immature birds in the combined samples from central coastal California from November through February was 60.1 per cent (N = 2343). This is significantly less (P < 0.001) than the fraction of immatures (68.8 per cent) in winter flocks at the northern boundary of the range during an approximately coincident period.

In the combined data from California and Washington, the composition of the winter populations (November through February) averaged 64.3 per cent immature birds (N = 4599) during this investigation. This closely approximates the value (64 per cent) estimated on the basis of a 75 per cent fledging success and negligible differential mortality in the postnuptial population, and appears to verify the accuracy of our estimates. However, a truly rigorous examination would require data from additional areas in the winter range.

SPRING MIGRATION

Spring migration of White-crowned Sparrows begins during the last half of April in the vicinity of Pullman, a few birds often appearing in the uplands by April 15. After this date, netting operations are shifted from the Snake River Canyon to the prairie near Pullman. The onset of migration is reflected in the data initially by samples with significantly greater (0.05 < P < 0.02) fractions of males (fig. 2). It is probable that this results from an augmentation of the proportion of males in the local population by predominantly male flocks arriving from the south. There is abundant and incontestable evidence from our own observation and from those of Oakeson (1954) and Irving (1960) that the initial flocks that arrive in the breeding areas contain only males, and that the first females may not arrive until as much as two weeks later. It seems probable that this time differential in the vernal migration of the sexes may be expressed at the latitude of Pullman, also. In Georgia, Odum (1949) has observed that female *Zonotrichia albicollis* tend to leave the winter area later than males.

Late in migration, the proportion of males decreased until the mean sex ratio in the last flocks to be sampled did not differ significantly from unity. It is noteworthy, however, that the fraction of males did not decline to the minimum (about 25 per cent) observed in autumn. The possible causes of this are too diverse to be identified with our limited data. However, the existence of such a lag suggests that the temporal and geographic patterns of spring migration in the two sexes may be different than the patterns of the autumn. In *Zonotrichia albicollis*, on the other hand, Millar (MS) found that the shift in sex ratio was greater during spring migration.

SUMMARY AND CONCLUSIONS

Populations of White-crowned Sparrows of the race *Zonotrichia leucophrys gambelii* were sampled during migration and on the wintering grounds in southeastern Washington and in central California, and on the breeding grounds in central Alaska. The data are analyzed in terms of seasonal changes in the proportions of adult and of immature birds and of males and females within each age class.

On the breeding grounds near Fairbanks, Alaska, the sex ratio in adults did not

differ significantly from unity during the postnuptial period in 1961; the mean values for immature birds may indicate a slight preponderance of males. The postnuptial population near Fairbanks probably contained between 60 and 70 per cent immature birds.

During autumn migration through southeastern Washington, near the northern margin of the winter range, the combined data for 12 years reveal a steady increase in the proportion of males in the samples during the migratory season, varying from about 25 per cent males at the beginning of migration to about 55 per cent males at the end of migration for both adult and immature birds. Although the pattern is interpreted as indicative of a later migration of males in both age classes, use of a hypothetical model shows that data obtained at only a single site cannot verify this interpretation. The differential migration of the sexes in autumn could be geographic, temporal, or both.

On the average, samples of migrant flocks in southeastern Washington contain between 70 and 80 per cent immature birds during most of the migratory period, increasing to about 85 per cent during the terminal days of migration. However, there is considerable annual variation in age ratio. The most obvious interpretation of this is that it reflects a delayed migration of at least part of the immature population. Nevertheless, alternative explanations involving geographic rather than temporal differentiation are equally valid.

On the wintering grounds in the Snake River Canyon in southeastern Washington, the population was stable at about 80 per cent males from November through March. There were no statistically significant differences in the sex ratio in the two age classes. This indicates a sexual segregation during winter, the females of both age classes tending to spend the winter farther south. Our samples from California plus additional data from the literature and from museum specimens confirm this and suggest also that females may tend to winter predominantly east of the Sierra Nevada and in northwestern México.

On the average, the winter population in the Snake River Canyon contained about 70 per cent immature birds. Winter populations in central California approximated 60 per cent immatures.

Spring migration in southeastern Washington began with flocks consisting of approximating 95 per cent males. At the end of migration the sex ratio had decreased to approximately 50 per cent males. Presumably this change resulted from an earlier or more rapid migration of males. The first flocks to arrive in central Alaska consist exclusively of males. The earliest females may not arrive until two weeks later.

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