LATITUDINAL VARIATION OF POSTNUPTIAL MOLT IN PACIFIC COAST WHITE-CROWNED SPARROWS

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ABSTRACT.—The duration of postnuptial molt in the White-crowned Sparrows of the Pacific Seaboard (*Zonotrichia leucophrys nuttalli* and *Z. l. pugetensis*) decreases northward by an average of 2.6 days per degree of latitude between the southernmost (35.2°N, molt duration 83 days) and northernmost (48.9°N, 47 days) limits of the breeding range. Males begin molting earlier than females by as much as 2 weeks. For both sexes, the date on which molt begins is independent of latitude and is correlated with the end of nesting season.—*Avian Biology Laboratory, San Jose State University, San Jose, California 95192, and Department of Zoology, Washington State University, Pullman, Washington 99164.* Accepted 22 June 1976.

IT is common knowledge, in part formalized in the "Bioclimatic Rule" (Hopkins 1920), that phenological development is delayed and the growing season is shortened as latitude and altitude increase. Animals must adapt their annual cycles accordingly, adjusting the allocation of time and energy to essential cyclic processes. Reproduction and the postnuptial molt are prominent cyclic processes that must be undertaken within a progressively shorter and later season as the latitude or altitude of the breeding grounds increases, but with few exceptions (e.g. Dolnik and Blyumental 1967, Flegg and Cox 1969, Noskov 1975) little is known of the temporal adjustments of molt in relation to latitude. To assist in alleviating this hiatus, we report here an investigation of the postnuptial molt of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli* and *Z. l. pugetensis*) that breed along the Pacific Coast of North America from about 34.5° to about 50°N. *Zonotrichia leucophrys nuttalli* is nonmigratory, and *pugetensis* is a short-distance migrant that intergrades with *nuttalli* in northern California (Blanchard 1941, Banks 1964, Mewaldt et al. 1968).

SAMPLE SITES AND METHODS

White-crowned Sparrows were captured with mist nets on their coastal nesting grounds at several localities (Fig. 1) from Pismo Beach, California (35.2°N), to Sidney, Vancouver Island, British Columbia (48.9°N). The birds were taken to San Jose, California (37.4°N), and housed together in outdoor aviaries (3.6 × 2.5 × 2.0 m) where they were subjected to essentially normal weather and photoperiod. The conditions of husbandry were as described by Mewaldt et al. (1968). Each bird was examined at the time of capture and weekly thereafter for the condition of molt in remiges, rectrices, coverts, body, and crown.

RESULTS AND DISCUSSION

Duration of postnuptial molt.—The duration of postnuptial molt decreases as an ostensibly linear function of latitude north of Pismo Beach (Fig. 2), following the least-squares regression

$$Y \text{ (days)} = 174.5 - 2.612X \text{ (°lat)} \qquad (1)$$

with n = 139, $S_{yx} = 11.29$, and $S_b = 0.2782$. The correlation coefficient is highly significant ($r = 0.628$, $P < 0.001$), and the latitudinal effect explains about 40% ($r^2 = 0.394$) of the statistical variability. On the average, the period of the postnuptial molt in individuals shortens by 2.6 days per degree of latitude northward (from 83 days at Pismo Beach to 47 days at Sidney). For a subset of birds that were studied

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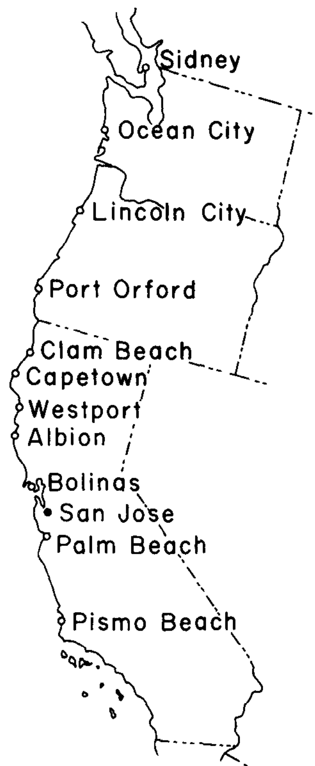

Fig. 1. Breeding-ground capture sites of White-crowned Sparrows transported to San Jose for observation. The transition between *Zonotrichia leucophrys nuttalli* (south) and *Z. l. pugetensis* (north) occurs at about the latitude of Capetown.

during both the first and second molting seasons in captivity, the regression equations differ significantly in elevation ($F = 6.28$, d.f. $= 1{,}68$, $P < 0.025$) but not in slope ($F = 0.52$, d.f. $= 1{,}68$, $P > 0.25$):

$$\text{Year 1: } Y = 172.3 - 2.537X \tag{2}$$

$$\text{Year 2: } Y = 150.1 - 2.054X \tag{3}$$

Although statistically significant, the difference between years is nevertheless slight. The predicted duration of molt at Pismo Beach in year 1 is 84 days, and in year 2 is 78 days. At Sidney, the predictions are 49 days in both years. These estimates compare with 83 days and 47 days for the same localities, respectively, estimated for all birds in year 1 by equation 1. In other words, the duration of molt as a function of latitude was virtually the same in both years of captivity.

We have only one independent estimate of the duration of postnuptial molt in free-living populations, and can therefore examine the accuracy of equation 1 as extrapolated to free-living birds only in terms of the elevation of the regression, but not in terms of slope. The duration of molt in free-living *nuttalli* at Bolinas, averaged for 5 consecutive seasons, was 68 days (Mewaldt and King, MS), or 8.8% less than the 74 days estimated from equation 1. In view of the local variability of molt particularly at the lower latitudes (Fig. 2), we regard this as very good agreement

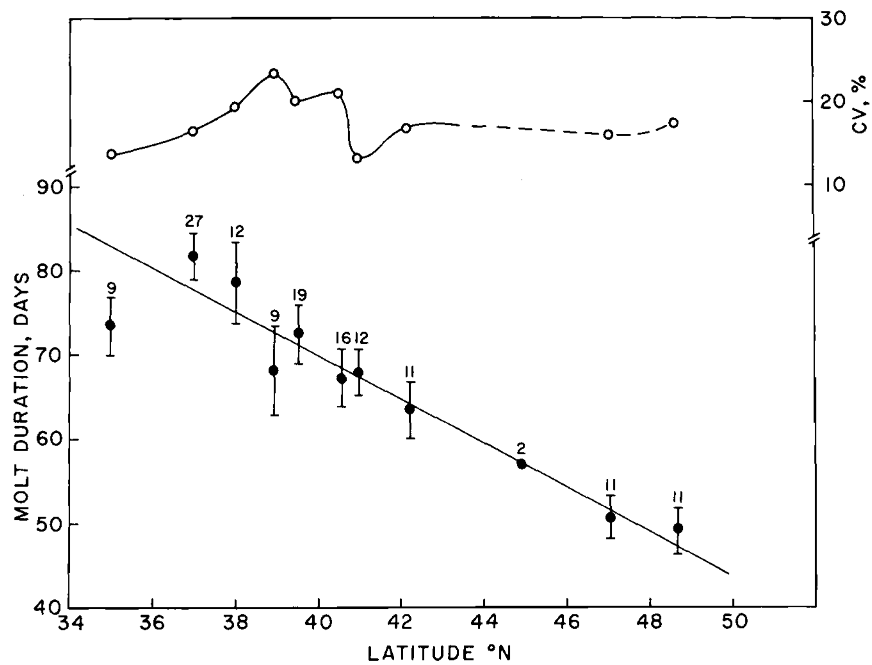

Fig. 2. Mean duration of postnuptial molt in relation to the latitude of the sample sites depicted in Fig. 1. Vertical bars show 1 SE above and below the mean; numerals show sample size. The least-square regression equation was computed from the individual data points (n = 139). The coefficient of variation is shown in the upper part of the figure.

that supports the accuracy of equation 1 as an estimator of the duration of molt in the free-living populations. This conforms with the results of similar comparisons of captive and free-living birds reported by Morton et al. (1969), Newton (1969), and King (1972). The apparently minor effects of captivity on the duration of molt, even at a site remote from the native locale, indicate that this trait in *Z. leucophrys* has a strong genetic basis that is affected only slightly, if at all, by environmental variables, including the trauma and the nutritional advantage of captivity. The data of Gwinner (1973) for the sylviid warblers *Phylloscopus trochilus* and *Ph. collybita* exposed to natural and artificial photoperiods in captivity are consistent with this conclusion.

Relative variability in the duration of molt as expressed by the coefficient of variation (CV = 100 SD/mean) ranges between about 10 and 23% in the samples. Between Pismo Beach and Westport, the CV increases to a maximum that remains

TABLE 1

ESTIMATED DATE ON WHICH POSTNUPTIAL MOLT BEGAN IN MALE AND FEMALE WHITE-CROWNED SPARROWS (SELECTED SITES)[1]

Sample site	Latitude	Males	Females
Westport	39.6°N	22 Jul ± 2.2 (7)	4 Aug ± 5.7 (8)
Capetown	40.5	25 Jul ± 1.4 (6)	6 Aug ± 4.5 (7)
Clam Beach	40.9	20 Jul ± 3.3 (8)	23 Jul ± 3.6 (6)
Ocean City	47.1	20 Jul (4)	2 Aug (4)

[1] Mean ± SE (n).

TABLE 2
ESTIMATED DATE ON WHICH POSTNUPTIAL MOLT BEGAN IN WHITE-CROWNED SPARROWS (SEXES COMBINED) IN RELATION TO LATITUDE[1]

Sample site	Latitude	Year 1	Year 2
Pismo Beach	35.1°N	13 Jul ± 2.7 (5)	24 May (4)
Palm Beach	36.9	3 Jul ± 3.4 (11)	21 May ± 2.4 (10)
Bolinas	38.0	22 Jul ± 2.1 (12)	—
Albion	39.2	30 Jul ± 4.5 (9)	—
Westport	39.6	29 Jul ± 3.5 (15)	13 Jun (4)
Capetown	40.5	1 Aug ± 3.1 (13)	13 Jun (3)
Clam Beach	40.9	19 Jul ± 2.8 (17)	19 Jun ± 2.3 (5)
Lincoln City	44.9	2 Aug (3)	28 Jun ± 1.7 (15)
Ocean City	47.1	27 Jul ± 2.8 (8)	—
Sidney	48.7	20 Jul ± 4.8 (6)	22 Jun ± 8.1 (5)

[1] Mean ± SE (n); year 1 = natural cycle, year 2 = first season in captivity.

at or above 20% northward to the latitude of Clam Beach, and then abruptly drops (Fig. 2). This peak in CV is centered near Cape Mendocino, regarded by Banks (1964) and Mewaldt et al. (1968) as the zone of morphological and functional transition between *nuttalli* and *pugetensis*. North of Cape Mendocino the CV of our samples remains below 20% to the northern limit of the range of *pugetensis*. In contrast, morphometric traits of *Z. leucophrys* along the Pacific Coast show no consistent trends of CV (Banks 1964). Functional traits such as molt may be less conservative than morphological traits, and we suggest that the peak of molt variability near Cape Mendocino may reflect the results of gene flow in a zone of secondary contact between *nuttalli* and *pugetensis*, but until additional data become available any extensions of this speculation are premature.

The onset of postnuptial molt.—Most of our birds were captured soon after the postnuptial molt began, allowing us to extrapolate accurately to its initial date in the free-living individuals. At sites for which we have adequate samples, males consistently began to molt earlier than females by as much as 2 weeks (Table 1), which is common among many species of songbirds (e.g. Dhondt 1973, Morton and Welton 1973) but by no means universal (e.g. Evans et al. 1967, Snow 1969). The dates on which postnuptial molt began in White-crowned Sparrows during the first season of observation showed no latitudinal trend (Table 2). This is consistent with the results of independent studies of free-living populations in central California (15 July: Mewaldt and King, MS) and northern Washington (17 July: Lewis 1975). Likewise no consistent trends exist in the variance of the data, an unknown fraction of which results from unequal sex ratios among the samples (we had to combine the sexes to obtain useful sample sizes).

The average date molt began during the second season of study (captives) was abnormally advanced by an average of about 6 weeks, occurring from late May to late June, with an erratic trend toward delay northward (Table 2). The general advancement probably resulted from the deletion of nesting from the normal sequence of events in the second year, and the abnormal latitudinal trend may be correlated with the exposure of the various sample populations to a common photocycle at San Jose that differs from the photocycle of their natural habitats in spring and summer.

Comparisons with other species.—Data similar to ours are available for only a handful of species. Noskov (1975) found that the postnuptial molt of adult Chaffinches (*Fringilla coelebs*) required about 65 days north of 60° (Finland) and 70–80 days in the Ukraine and Crimea (south to about 45°). The onset of molt was progressively delayed by a maximum of about 2 weeks between the latitudinal extremes (with the exception of the anomalous "late" population in the Kurish Nehrung, also noted by Dolnik and Blyumental (1967), which may be correlated with the phenology of a maritime region). The latitudinal effect on the onset of molt in the Chaffinch was at least 0.4 days per degree of latitude, and at most 1 day per degree. This is much less than that found in the White-crowned Sparrow (2.6 days per degree). Haukioja (1971), by methods differing from Noskov's (1975), estimated that the postnuptial molt of the Chaffinch in Finland (59–64°N) required 70 days, which is the same as Newton (1968) found in Great Britain (50–54°N).

Several investigations based on data from the British Trust for Ornithology Moult Enquiry (Newton 1968, Snow 1969, Flegg and Cox 1969, Bell 1970, Ginn 1975) have revealed either no latitudinal differences in the timing and duration of molt (e.g. *Turdus merula, Prunella modularis*), or latitudinal differences in the date of onset but not duration (*Parus major*), or latitudinal differences in both onset and duration (*Parus caereulus*). Evans et al. (1967) reported that the start of postnuptial molt in *Carduelis flammea* occurred on essentially the same date in England (about 55°N) and northern Norway (about 70°N), and that the duration was shorter by 6 days in Norway in males but not females. Pitelka (1945) found that postnuptial molt required about 2 weeks less in northern forms of *Aphelocoma coerulescens* than in southern forms in the western United States (a latitudinal range of about 20°). King (1974) presented evidence indicating that the postnuptial molt of *Zonotrichia capensis australis* occurs on about the same schedule through about 15° of latitude in southern Argentina, but neither the methods nor the data were adequate to allow the detection of small (a few days) differences in duration or schedule.

Additional anecdotal or fragmentary reports (e.g. Stresemann and Stresemann 1970, Green and Summers 1975, on the molt of *Plectrophenax nivalis*), that need not be recounted here, conform with what is already evident from the foregoing summary. Latitudinal effects on the schedule and duration of postnuptial molt vary between species, no doubt reflecting the species-specific coevolution of the annual time budget and other life-history characteristics in response to environmental seasonality.

Phenology of the postnuptial molt in Pacific Coastal White-crowned Sparrows.— The "Bioclimatic Rule" predicts that vernal phenological development at Sidney (48.7°N) will lag behind that at Pismo Beach (35.1°N) by 41–54 days. The lower limit of this range corresponds with the phenological map presented by Caprio et al. (1974). The onset of postnuptial molt does not follow this trend, being practically independent of latitude (Table 2). This illuminates a point that might have been apparent a priori, namely that the date on which molt begins depends on the termination of nesting. This occurs in mid-July in the *nuttalli-pugetensis* complex in both central California (Mewaldt and King, MS) and northern Washington (Lewis 1975). The shortened *duration* of molt northward, however, is clearly an adaptation to the progressively shorter season of favorable trophic and climatic conditions. Phenological investigations in western North America are in their infancy (Caprio et al. 1974), and for a crude index of environmental seasonality we have to rely on estimates of the frost-free period. From the summary of first and last killing frosts in the *Yearbook of Agriculture* (USDA 1941) we selected 31 sites representing the breeding grounds of *nuttalli-pugetensis*. The relationship between the frost-free period and latitude (34–50°N) is apparently linear, following the equation

$$Y \text{ (days)} = 586.8 - 7.83X \text{ (°lat)} \quad (4)$$

and having, as expected, substantial variation ($S_{yx} = 61.66$, $S_b = 1.446$). On the average, the frost-free season decreases by 120 days northward within the breeding range of the *nuttalli-pugetensis* complex. The northward decrease in the duration of molt is one adaptive response to this temporal restriction. The significance of this cannot be fully understood apart from a detailed analysis of the annual time budgets of the populations. This extends beyond the logical limits of this brief report, and will be presented as a separate account.

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