Condor, 80:222–229

EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON POSTNUPTIAL MOLT IN CAPTIVE WHITE-CROWNED SPARROWS

JOHN D. CHILGREN

The annual cycle of the White-crowned Sparrow (*Zonotrichia leucophrys*) and its regulation have been intensively studied with respect to reproduction and migration (e.g., DeWolfe 1967, 1968, Farner and Lewis 1971, King 1972a, Morton et al. 1972, Lewis and Farner 1973). Nevertheless, the environmental control of molt is poorly understood. Several experimental studies of molt in captive birds have been performed under artificial conditions or in natural environments distant from the site where molt would naturally occur (e.g., Eyster 1954, Helms 1968, Pohl 1971, Gwinner 1973). Studies of temperate zone species were expedited by the induction of molt through manipulation of the daily photoperiod (e.g., Eyster 1954, Wolfson 1954, Farner 1964, Blackmore 1969). To be meaningful, any laboratory study of molt must reveal basic similarities in molt pattern, tempo, and timing between captives and free-living populations.

I wished to determine how abiotic factors affect molt and how natural and artificially-induced molts compare with those of free-living birds. To do so I examined the postnuptial molt of migratory White-crowned Sparrows (*Z. l. gambelii*) maintained outdoors at two different latitudes and indoors at different air temperatures and photoperiods. My investigation began with a study of how to elicit a typical postnuptial molt under controlled environmental conditions. Once achieved, I studied the onset and progress of molt when some of those conditions were varied. Earlier analyses of postnuptial molt in this species (Morton et al. 1969) provided a basis for comparison between experimentally-induced molt and molt of free-living birds, and also for a comparison of the annual variation in molt chronology between different populations of *gambelii*. This report will therefore consider the effects of various temperatures and photoperiods on the duration and rate of postnuptial molt.

METHODS

White-crowned Sparrows were captured with mist-nets near Pullman, Washington (46°46′N) and kept in outdoor aviaries up to a year (until December 1971) at Washington State University. They were then divided into three groups and transferred to constant temperature rooms (20°C) and held one bird per cage. Group E20S (experimental, 20°C, short photoperiod) was given a 12L:12D photoperiod. Groups E20 (intermediate photoperiod) and E20L (long photoperiod) were given 16L:8D and 20L:4D photoperiods, respectively. In groups that molted, the progress of molt was recorded and the growth of primaries 5 and 9 was measured daily at about 10:00. These three groups of birds were used to determine which of the three photoperiods would elicit a typical molt.

Other birds captured near Pullman or in central Washington and kept up to a year in outdoor aviaries were divided into four groups. Members of group CP (control, outdoors, Pullman) were individually caged in an aviary shielded from direct sunlight. Groups E5, E15, and E25 comprised birds placed indoors at 5°, 15°, and 25°C, respectively, each with a 16L:8D photoperiod.

Birds of group CF (control, outdoors, Fairbanks) were captured in June 1973 and caged separately in a screened outdoor shelter covered by a translucent fiberglass roof. The shelter was partially shaded by a grove of trees. Molt progress was charted every other day, while primaries 1, 5, and 9 were measured daily between 16:00 and 17:00. Table 1 summarizes the treatments of all these groups of birds.

The length of a molting feather was measured until the keratin sheath was no longer evident or could be removed by a gentle touch. This endpoint seemed preferable to that in which the absence of blood in the calamus indicates completed growth, as I found that primary wing feathers continued to grow 1 to 3 mm farther even though blood was no longer visible in the calamus. Feather groups monitored included primaries 1–9, secondaries 1–6, secondaries 7–9 (tertials), rectrices, crown, and body feathers. The duration of molt was also derived from these data. In this report, I have lumped data for all secondary remiges and omitted data for crown feathers and rectrices. Lighting for all indoor birds was provided by 40-watt incandescent lamps placed about 30 cm above each cage.

RESULTS AND DISCUSSION

SELECTION OF AN APPROPRIATE PHOTOPERIOD

Of the three groups, E20S, E20 and E20L, only group E20S failed to molt within 95 days. This result is supported by recent experiments at the University of Washington, which showed that *gambelii* did not molt within four years at a photoperiod of 12L:12D (R. A. Lewis, pers. comm.). In groups E20 and E20L, prenuptial molt was apparently skipped, unlike the normal molt sequence observed in northern free-living populations of White-crowned Spar-

TABLE 1. Photoperiod and air temperature treatments of different captive bird groups.

Group	N	Treatment	Treatment period
CP	4	outdoors, Pullman	28 May 72– 5 Aug 72
CF	7	outdoors, Fairbanks	28 Jun 73– 5 Sep 73
E20S	12	12L:12D, 20°C	12 Dec 71–17 Mar 72
E20	17	16L:8D, 20°C	12 Dec 71–17 Mar 72
E20L	9	20L:4D, 20°C	12 Dec 71–17 Mar 72
E5	6	16L:8D, 5°C	3 Mar 73– 5 Sep 73
E15	5	16L:8D, 15°C	26 Mar 72– 5 Aug 72
E25	6	16L:8D, 25°C	4 Mar 73– 2 Aug 73

rows. From the day this experiment was initiated, group E20L began to molt in 54.6 ± 2.97 ($\pm$ SD) days compared with 69.9 ± 6.67 days for group E20 ($P < 0.05$; 95% confidence intervals are 52.3–56.9 and 66.5–77.3 respectively). A study by Dolnik (1975) shows parallel findings. In an investigation of the photoperiodic control of molt, fat deposition, body weight, and reproductive condition in the migratory Chaffinch (*Fringilla coelebs*), Dolnik subjected males to five different photoperiods (photophases of 20L, 18L, 16L, 14L, and 12L) beginning 3 January. His results showed an earlier molt onset with longer photoperiods. The mean temporal difference between molt onset in 20L and in 16L birds was 15 days, the same as I observed in White-crowned Sparrows.

The mechanism responsible for these photoperiodic effects in the White-crowned Sparrow is probably similar to that in the Chaffinch, which also breeds at high latitudes (ca. 55–62°N). Photorefractoriness ceases during the short days of winter (e.g. Lofts and Murton 1968). Artificially long photoperiods in December or January accelerate breeding development (gonadal recrudescence; development of cloacal protuberance in males), the rate of which is a function of the photoperiod duration. Birds that develop more rapidly enter the refractory phase sooner. Consequently, those birds whose gonads have regressed to a level compatible with the onset of postnuptial molt will undergo molt earlier. Since Dolnik calculated that molt in the Chaffinch begins 47 days after the end of the period of photosensitivity, the beginning of which is determined by the duration of photoperiod, molt can be expected to occur earlier in birds exposed to longer photoperiods. There are two other relevant aspects of Dolnik's study. First, the Chaffinch molt occurs under 12L:12D, but only after five months. Second, the molt normally requires about 90 days, but is shortened by as much as 43 days under 12L:12D, compared to 89 days under 20L:4D. Furthermore, molt in weakly photostimulated birds "catches up" with that of strongly stimulated birds and ends at about the same time in 14L birds as in 20L birds. Under 12L, the molt finishes about one month later. Whether females will respond similarly is unknown for either species. I did not determine the sex of birds in groups E20 and E20L, although I must assume that due to chance factors involved in capture and selection, females were present in both groups.

No significant differences in molt duration of any feather category were found between groups E20 and E20L, although the mean duration of group E20L tended to be longer in most plumage categories. Group E20L did, however, exhibit consistently greater variability in molt duration (see Figs. 1 to 4) and showed frequent irregularities in molt sequence. These results indicated that the intermediate photoperiod (16L:8D) was the better choice for subsequent indoor experiments. The phase advance of molt onset in group E20L relative to group E20 resembles the effect of warm temperature in advancing postnuptial molt onset in White-crowned Sparrows (Chilgren 1977), but without an attendant variability in molt tempo. Gavrilov and Dolnik (1974) found that warmth (26°C) delayed molt in the Chaffinch by about 12 days compared with cold (7°C). Evidently, passerines differ in their responses to temperature with respect to molt onset.

It is premature to suggest schemes that relate photoperiodic mechanisms controlling the onset or duration of molt to other seasonal cycles (as has been done for the Chaffinch). However, my data indicate that unnaturally long photoperiods given out of season elicit irregularities in molt tempo and pattern. In this context, it is significant that the variation in molt duration in nearly all plumage classes of group E25 was almost as great as that observed for group E20L (see Figs. 1 to 4). This suggests that high temperature in addition to extended photoperiods may desynchronize the phasing of molt onset in individual birds.

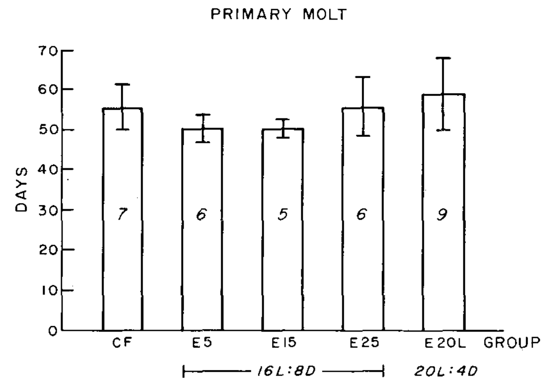

FIGURE 1. Duration of primary molt. Numbers within bars are sample sizes. Vertical lines indicate one standard deviation. See Table 1 for meaning of group designations.

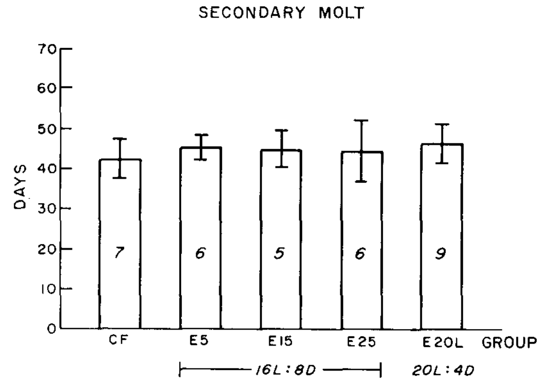

FIGURE 2. Duration of secondary molt. Explanations as in Figure 1.

EFFECTS OF TEMPERATURE AND LATITUDE ON POSTNUPTIAL MOLT

The duration of postnuptial molt in other bird groups is shown in Figures 1 to 4. Data for groups CP and E20 are omitted, because they were equivalent to data for groups CF and E25, with one exception. Only one major difference in molt times appears to be of possible functional significance. A one-way analysis of variance (AOV) followed by a Student-Neuman-Keuls' test (Steel and Torrie 1960) showed that the complete molt of group E5 was significantly less than other indoor groups ($P < 0.05$) but not different from group CF if the latter is included in the AOV. The basis for this difference was not found in the molt duration of any feather category examined. Two further analyses, however, afford at least a partial explanation. The results of these analyses are presented in Tables 2 and 3. Table 2 shows that in five of the eight shedding intervals for groups E5 and E15, the means rank first or second compared with other indoor birds; the means of group E25 rank third or fourth in five of the shedding intervals, with group E20 containing intermediate values; and the sums of the means for each indoor group form a graded series with the lowest in group E5 and the highest in group E25. The shedding intervals for group CP are consistently smaller than those of group CF; therefore the sum of the means for group CP is less than that for group CF, suggesting a shorter molt of the primaries in group CP than in group CF (compare 42.5 ± 3.9 days with 55.8 ± 7.4 days; *t*-test: $P < 0.05$). Duration of complete molt was about the same in both groups (a mean difference of three days). This was the only difference between groups CP and CF.

Although the data of Table 2 indicate that cooler temperatures reduce the shedding interval of primary remiges, primary molt duration was not significantly different among any of the indoor groups. Thus, differences in the shedding interval alone are not a sufficiently convincing aspect of the temperature-induced differences in the duration of complete molt. This problem is better resolved with data in Table 3, which show that temporal phase relationships between molt onset in primary and secondary remiges or primaries and body

TABLE 2. Variation in the mean shedding interval between adjacent primary remiges during postnuptial molt.[1]

Primary set	Group CP (N = 4)	Group CF (N = 7)	Group E5 (N = 6)	Group E15 (N = 5)	Group E20 (N = 17)	Group E25 (N = 6)
1–2	1.20 ± 1.10	1.43 ± 0.43	0.67 ± 0.82	0.40 ± 0.55	1.71 ± 0.59	2.14 ± 0.90
2–3	1.80 ± 1.79	3.14 ± 1.46	2.17 ± 0.98	1.80 ± 0.45	2.24 ± 0.97	1.86 ± 0.38
3–4	2.50 ± 1.91	2.67 ± 1.03	3.33 ± 1.02	2.40 ± 1.67	2.88 ± 1.50	2.40 ± 1.67
4–5	3.50 ± 2.50	5.00 ± 1.10	2.67 ± 2.06	4.00 ± 1.41	3.13 ± 1.59	3.14 ± 1.57
5–6	2.00 ± 0.00	4.43 ± 1.81	3.33 ± 1.63	4.40 ± 0.89	3.88 ± 1.36	4.29 ± 2.14
6–7	4.50 ± 1.91	5.71 ± 0.76	5.00 ± 2.10	4.40 ± 0.92	4.67 ± 1.53	5.33 ± 1.63
7–8	3.00 ± 1.15	4.00 ± 2.00	3.33 ± 1.03	4.60 ± 1.67	4.29 ± 1.56	5.00 ± 1.10
8–9	2.50 ± 1.00	2.71 ± 1.60	2.00 ± 0.00	2.20 ± 1.10	3.00 ± 1.27	4.29 ± 1.86
Σ means	21.0	29.1	22.5	24.2	25.8	28.5

[1] Mean days ± standard deviation; refer to Table 1 for treatment conditions.

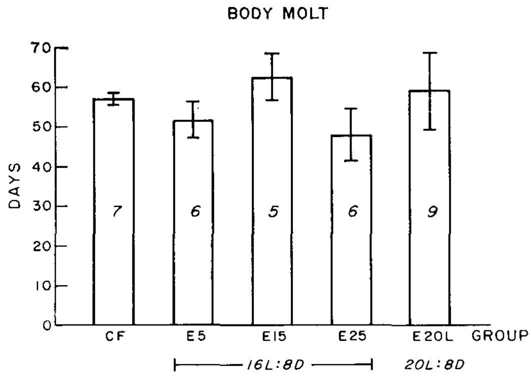

FIGURE 3. Duration of body molt. Explanations as in Figure 1.

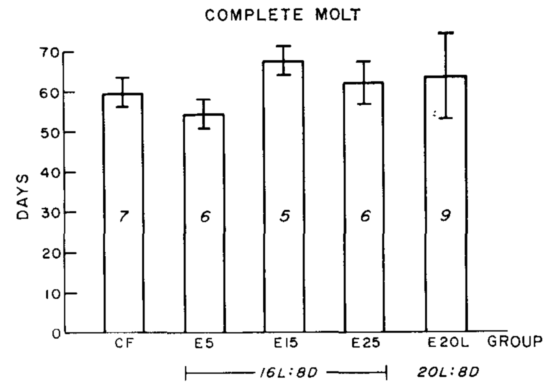

FIGURE 4. Duration of complete molt. Explanations as in Figure 1.

feathers in group E5 tend to differ from other indoor groups. An AOV performed for each column in Table 3 (but excluding in each the all-female, small and highly variable group CP) showed that no significant treatment effects existed for the tail feathers ($P < 0.10$) but that significant differences appeared for the secondary feathers ($P < 0.05$) and body feathers ($P < 0.005$). Identification of significant means within these last two categories by the Student-Newman-Keuls' ($\alpha = 5\%$) indicated that for secondary feathers, group E5 was significantly different from only group E20 despite higher means for groups E15 and E20L. This resulted from the inadequate sample sizes for groups other than E20. Nevertheless, a temperature effect is indicated. With regard to body feather molt, groups E5, E15, and CF were significantly different from group E20, but not from groups E20L or E25; group E15 and CF means were different from those of 8 days or more. These results are conceptually satisfying as cold temperature might be expected to accelerate some aspect of molt, thereby reducing the time unfeathered portions of the integuments are exposed. In this manner, a molting bird conserves body heat that would be lost by maintaining a steeper thermal gradient between skin and air for a longer period of time.

A comparison of outdoor groups shows some profound differences in the phasing of molt onset (Table 3). These differences are probably best explained by the uniqueness of each original population. Individuals of group CP were entirely female and captured in central Washington, whereas those of group CF were of mixed sex and captured near College, Alaska.

The data in Table 2 confirm the estimated mean shedding interval for feathers of primary set 1–5, 3–7, and 5–9 reported earlier (Morton et al. 1969). For all groups studied, replacement (in days) was most rapid between primaries 1–2 (1.26 ± 0.65), intermediate in primaries 2–3 (2.17 ± 0.51), 3–4 (2.70 ± 0.36), and 8–9 (2.78 ± 0.82), and slowest in primaries 4–5 (3.75 ± 0.83), 5–6 (3.72 ± 0.94), 6–7 (4.94 ± 0.51) and 7–8 (4.04 ± 0.76).

King (1972b) has studied molt in the Rufous-collared Sparrow (*Zonotrichia capensis hypoleuca*) of equatorial and subequatorial regions. The shedding intervals in primary molt of this species merit comparison with those for White-crowned Sparrows. The shedding interval in the latter is short initially and

TABLE 3. Elapsed time between molt onset in primary feathers and secondary, tail, or body feathers.[1]

Group	Secondaries	Tail	Body
E5	8.83 ± 3.43 (6)^{a}	5.50 ± 2.74 (6)^{a}	4.33 ± 3.39 (6)^{ab}
E15	13.80 ± 3.56 (5)^{ab}	6.20 ± 1.92 (5)^{a}	1.40 ± 4.02 (5)^{a}
E20	13.38 ± 5.26 (16)^{b}	9.06 ± 3.34 (16)^{a}	8.77 ± 4.87 (15)^{c}
E20L	14.50 ± 4.81 (8)^{ab}	10.43 ± 5.32 (7)^{a}	8.00 ± 5.51 (6)^{bc}
E25	12.41 ± 3.08 (6)^{ab}	9.57 ± 2.57 (6)^{a}	8.00 ± 2.00 (6)^{bc}
CP[2]	8.00 ± 4.97 (4)	5.60 ± 5.70 (4)^{a}	-3.80 ± 6.72[3](4)
CF	14.86 ± 3.18 (7)^{ab}	5.43 ± 7.04 (7)^{a}	1.00 ± 3.74 (7)^{a}

[1] Mean days $\pm$ standard deviation (N in parentheses).
[a] $P < 0.05$ between means with different letter superscripts (compare vertically); significance based on 1-way analysis of variance with a Student-Neuman-Keuls' test for separation of significant means.
[2] This group excluded from the analysis of variance (see text).
[3] Negative sign indicates mean day of body molt onset preceeded primary molt onset.

TABLE 4. The effect of photoperiod on primary remex growth rates during postnuptial molt in captive White-crowned Sparrows.[1]

Primary number	Measurement period	Photoperiod		
		20L:4D (Group E20L)	16L:8D (Group E20)	Natural (Group CF)
1	Days 1–9	—	—	3.93 (0.55)
	Throughout	—	—	2.76 ± 0.15[2]
5	Days 1–9	3.98 (0.30)	4.12 (0.47)	4.03 (0.98)
	Throughout	2.86 ± 0.22	2.99 ± 0.17	3.04 ± 0.29
9	Days 1–9	3.08 (0.55)	3.07 (0.94)	3.15 (0.70)
	Throughout	2.35 ± 0.13	2.34 ± 0.19	2.32 ± 0.11

[1] Mean growth rate in mm/day ($s_{y.x}$ in parentheses).
[2] Mean growth rate ± standard deviation.

increases to nearly five days between primaries 6–7, but it is then shortened for the remaining primaries. The pattern in Rufous-collared Sparrows is similar except for pauses in the sequence between primaries 3–4 and 6–7. The significance of these differences is not evident.

MOLT IN ALASKAN WHITE-CROWNED SPARROWS

The following sections describe the onset of molt in various pterylae and the rates of feather growth in group CF, which contained Alaskan birds captured shortly before the time of their natural molt. When appropriate, allusions will be made to indoor groups of experimental birds.

Molt of primary remiges. The primaries of group CF began to molt on 6 July ± 2.6 days. The elapsed time between the appearance of P1 and P9 in all six experimental groups was 25.2 ± 3.23 days. The mean growth rate throughout the molt of P1 was 2.76 mm/day and 3.93 mm/day for the period of most rapid growth (equivalent to days 1–9, as computed from a least squares plot to ascertain maximum slope), after which the rate asymptotically approached zero (see Table 4). The fastest growth rate is apparently unaffected by daylength exceeding 16 h. Measurements of growth rates of P5 and P9 of birds under 16L:8D (group E20) and 20L:4D (group E20L) were not significantly different from those of group CF. For the first nine-day period, the growth rates of P5 in groups E20 and E20L were similar, but were about 32% faster compared with P9. For primaries 5 and 9, group CF showed growth rates similar to those of groups E20 and E20L. Whether shorter photoperiods would affect growth rates of individual feathers is unknown. The data previously discussed (viz., the similarities in primary shedding intervals and in molt duration in various pterylae of birds under different experimental conditions) show that no substantial differences in feather growth rates exist among the groups of birds studied. Measurements of individual feathers confirm that growth rates of feathers are not influenced by moderate or long photoperiods. Instead, they appear to be unalterable under conditions of adequate nutrition and some brief but undefined, photoperiod. It is not clear whether populational differences in growth rates of individual feathers are accountable genetically or reflect changes in the physical environment at some relatively flexible point in an otherwise highly structured annual cycle.

Molt of secondary remiges. Secondary feathers of group CF began to molt on 19 July ± 4.7 days. Analyzing the secondary molt in 52 captives, I found that the focus of molt was limited to S8, S9, or S1, but seldom S7 (once in 52 cases). Table 5 shows the most common sequences found in molting secondaries. From beginning to end, the most common sequence was S8, S7, S1, S9, S2, S3, and lastly S4-S5-S6 in any order but commonly ending in S5. In the Mountain White-crowned Sparrow (*Z. l. oriantha*), the order of secondary remex appearance differs slightly, the sequence being S8, S7, S9, S1, S6, S3–5 (Morton and Welton 1973). Thus the secondary remex sequences of these two taxa are least similar in the position of S6. Definitive molt sequences in secondary flight feathers of other White-crowned Sparrows might be useful for distinguishing populations of this species.

The duration of molt of all secondary remiges was about 40 days in all groups studied. Occasionally, two secondaries were shed within a 24 h period.

Molt of rectrices. Molt of the tail feathers was the most irregular of all the tracts studied and the most difficult to assess, since rectrices are highly susceptible to damage in caged birds. The mean day of molt onset in group CF was 11 July ± 9.1 days. Rectrices also required about 40 days to grow to completion, but only 35 days in *Z. l. oriantha* (Morton and Welton 1973). Simultaneous loss of R1 to R6 on one side did not affect the natural centrifugal order of replacement in the intact group. The shedding interval of birds examined was 2–3 days longer than that reported by Morton et al. (1969), i.e., often within three days.

Body molt. Body molt began on 6 July ± 2.6 days in group CF. These feathers may begin to molt before, after, or simultaneously with molt of primaries, but in group CF they began to molt shortly after the onset of primary molt (see Table 3). The duration of body molt was about 2.5 days less than the duration of the entire molt in both outdoor groups, but anywhere from 2 days (group E5) to 14 days (group E25) less in indoor groups.

TABLE 5. Frequency of emergence of secondary remiges as a function of their order of appearance during postnuptial molt.

Order of appearance	Secondary remex number	Occurrence (%) (N = 52)
First	8	85
	1 or 9	15
Second	7	65
	8	12
Third	1	37
	9	21
	7	21
Fourth	9	48
Fifth	2	79
Sixth	3	42
	6	14
Seventh to Ninth	4,5,6[1]	63

[1] Appearance in any order.

COMPARISONS WITH PAST STUDIES

There are no imporant differences between my findings in this study and those of Morton et al. (1969) with respect to calendar dates of molt onset in various feather groups of White-crowned Sparrows of Alaska. However, I found substantial differences in the molt duration of primary, secondary, and body feathers as well as in the rates of primary feather growth. Differences between my results and theirs may reflect to some extent differences in technique as well as in avian populations. Morton et al. (1969) did not measure primary feathers regularly and estimated growth rates of individual feathers from data taken at intervals of several days. Furthermore, the last day of growth was usually estimated (M. L. Morton, pers. comm.).

Morton et al. (1969) found that P1 grew at a rate of 0.62 mm/day throughout molt and 5.4 mm/day for P9. The rate for P1 was probably meant to be 6.2 mm/day since primary molt in their study lasted only 37 days and P1 must attain a length of at least 50 mm. Their growth rate for P9 was more than double what I found (Table 4). However, the mean length of P9 in birds they studied was 61.8 mm compared with 55.3 mm in group CF. Furthermore, the duration of molt of P9 for group CF was 23.9 ± 1.86 days, but was half this in the earlier study. Hence, the growth rates and molt duration of P9 appear to be substantially different in the two studies (which are 10 years apart). The rapid rate of primary growth reported by Morton et al. (1969) adequately explains the 19 mean-day difference in duration of primary molt between my study and theirs. In *Z. l. oriantha,* primary molt lasts about 46 days (Morton and Welton 1973), near the mean of both outdoor groups in this study. The Rufous-collared Sparrow shows rapid growth rates in primary remiges from 5.8 to 9.5 mm/day up to 60% of their maximum lengths (King 1972b). Despite such rates, the longer molt duration (about 80 days) in that species resulted from a protracted shedding interval of the primaries (about double that found in this study) and perhaps an extended body molt. Newton (1969) reported maximum growth rates of primaries at 4–5 mm/day in captive Common Redpolls (*Acanthis flammea*) and 3–4 mm/day for the rapid growth period of primaries in Bullfinches (*Pyrrhula pyrrhula*; Newton 1967). Breast feathers of chickens grow at rates of 2.5–3 mm/day (Lillie 1940).

The duration of secondary molt found by Morton et al. (1969) was 27.5 days compared with 40 days in this study. Hence, it appears that secondary remiges in my birds grew more slowly, although individual feather growth rates were not determined in either study. In *Z. l. oriantha* secondary molt lasts 38.3 days (Morton and Welton 1973) and hence growth rates are probably comparable to those in *Z. l. gambelii.*

Body feather molt and the complete molt lasted about 48 days as reported by Morton et al. (1969), six days shorter than the shortest mean duration found in both indoor and outdoor groups of birds in my study. DeWolfe (1967) estimated 33 days for the duration of molt in individuals, but no individual birds were studied. It may be questioned whether differences in findings among these studies reflect more than technical differences in assessing molt duration, although many of them appear to be real.

Postnuptial molt shows a pronounced latitudinal variation in the coastal races, *Z. l. nut-*

talli and *Z. l. pugetensis* (Mewaldt and King 1977). The molt lasts nearly as long the second year as it did the first year after capture, even though studied far from the sites of capture. This argues for a lesser variability in molt duration for *gambelii*, especially at the same latitude, even though these findings have no direct bearing on *gambelii*. The latitudinal range over which *gambelii* can be found in Canada and Alaska during the breeding period (see Cortopassi and Mewaldt 1965) is greater than that within which birds were used in the study by Mewaldt and King (ca. 14°). A study of molt in *gambelii* over a similar latitudinal range might therefore reveal comparable changes in molt chronology. The aforementioned differences in molt duration underscore the need for additional and continued observations of molt in postbreeding *gambelii* at various latitudes.

SUMMARY

Postnuptial molt was studied in two outdoor and six indoor groups of captive White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). Air temperature differed in four, and photoperiod differed in three of the indoor groups. Molt occurred in all groups except birds at 12L:12D. The most typical postnuptial molt was observed in groups at 16L:8D at 15° or 20°C. A 20L:4D photoperiod (20°C) hastened molt onset compared to a 16L:8D photoperiod (20°C), but resulted in lack of synchrony in molt onset in individuals (also occurring in birds at 16L:8D and 25°C). No differences in molt duration among feather tracts studied were found between birds at 20L:4D or 16L:8D.

Low air temperature (5°C) reduced the overall duration of molt, but not the molt of any of the six feather tracts examined. This appeared to be the result of at least two processes: (1) the shedding interval between adjacent primaries tended to be shorter in cold-acclimated birds, and (2) the phasing of molt onset in secondary and body feathers relative to primary feather molt onset was significantly altered under low to moderate (5–15°C) air temperature, favoring a shorter overall molt. Higher air temperatures had little or no effect upon molt tempo or chronology.

Primary wing feathers of captives subjected to 16 and 20 h photoperiods grew at the same rate as those of captives at the natural breeding site. The calendar dates of molt onset of postnuptial molt as well as molt onset in various feather tracts observed in this study did not differ from those in a study conducted 10 years earlier. However, substantial differences were found in growth rates of individual feathers, perhaps reflecting the less exact methodology of earlier investigations in addition to differences in avian populations.

ACKNOWLEDGMENTS

For critical review and commentary on previous drafts, I thank B. B. DeWolfe, J. R. King, R. A. Lewis, L. R. Mewaldt, and M. L. Morton. D. Robinson completed some of the molt measurements while I was in Alaska. I gratefully acknowledge the financial and moral support of J. R. King during my summer in Alaska. My research space there was kindly provided by G. C. West. This study was funded in part by grants from the U.S. National Science Foundation (GE-35651) and the U.S. National Institutes of Health (GM-1276-12), and was part of a doctoral dissertation submitted to Washington State University.

LITERATURE CITED

Blackmore, F. H. 1969. The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 30:433–444.

Chilgren, J. D. 1977. Body composition of captive White-crowned Sparrows during postnuptial molt. Auk 94:677–688.

Cortopassi, A. J., and L. R. Mewaldt. 1965. The circumannual distribution of White-crowned Sparrows. Bird-Banding 36:141–169.

DeWolfe, B. B. 1967. Biology of White-crowned Sparrows in late summer at College, Alaska. Condor 69:110–132.

DeWolfe, B. B. 1968. *Zonotrichia leucophrys gambelii* (Nuttall); Gambel's White-crowned Sparrow, p. 1324–1344. *In* O. L. Austin [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237, part 3.

Dolnik, V. R. 1975. Fotoperiodicheskiy kontrol' sezonnykh tsiklov vesa tela, lin'ki i polovoy aktivnosti u zyablikov (*Fringilla coelebs*). Zool. Zh. 54:1048–1056.

Eyster, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature and season on the activity of captive songbirds. Ecol. Monogr. 24:1–28.

Farner, D. S. 1964. The photoperiodic control of reproductive cycles in birds. Am. Sci. 52:137–156.

Farner, D. S., and R. A. Lewis. 1971. Photoperiodism and reproductive cycles in birds. Photophysiology 6:325–370.

Gavrilov, V. M., and V. R. Dolnik. 1974. Bioenergetika i reguliaciia poslebračnoj i postiuvennoj linek u ziablikov (*Fringilla coelebs coelebs*). Academiya Nauk SSSR 55:14–61.

Gwinner, E. 1973. Die Dauer der Grossfiedermauser beim Fitis (*Phylloscopus trochilus*) und beim Zilpzalp (*Ph. collybita*) unter verscheidenen photoperiodischen Bedingungen. J. Ornithol. 114:507–510.

Helms, C. W. 1968. Food, fat, and feathers. Am. Zool. 8:151–167.

King, J. R. 1972a. Adaptive periodic fat storage by birds. Proc. XV Int. Ornithol. Congr. (1970): 200–217.

KING, J. R. 1972b. Postnuptial and postjuvenal molt in Rufous-collared Sparrows in northwestern Argentina. Condor 74:5–16.

LEWIS, R. A., AND D. S. FARNER. 1973. Temperature modulation of photoperiodically induced vernal phenomena in White-crowned Sparrows (*Zonotrichia leucophrys*). Condor 75:279–286.

LILLIE, F. R. 1940. Physiology of development of the feather. III. Growth of the mesodermal constituents and blood circulation in the pulp. Physiol. Zool. 13:143–201.

LOFTS, B., AND R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool. (Lond.) 155:327–394.

MEWALDT, L. R., AND J. R. KING. 1978. Latitudinal variation of postnuptial molt in White-crowned Sparrows of the Pacific Coast. Auk 95:168–174.

MORTON, M. L., J. L. HORSTMANN, AND J. M. OSBORN. 1972. Reproductive cycle and nesting success of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. Condor 74:152–163.

MORTON, M. L., J. R. KING, AND D. S. FARNER. 1969. Postnuptial and postjuvenal molt in White-crowned Sparrows in central Alaska. Condor 71: 376–385.

MORTON, M. L., AND D. W. WELTON. 1973. Postnuptial molt and its relation to reproductive cycle and body weight in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*). Condor 75:184–189.

NEWTON, I. 1967. Feather growth and moult in some captive finches. Bird Study 14:10–24.

NEWTON, I. 1969. Moults and weights of captive Redpolls, *Carduelis flammea*. J. Ornithol. 110: 53–61.

POHL, H. 1971. Seasonal variation in metabolic functions of Bramblings. Ibis 113:185–193.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

WOLFSON, A. 1954. Production of repeated gonadal, fat, and molt cycles within one year in the Junco and White-crowned Sparrow by manipulation of daylength. J. Exp. Zool. 125:355–376.

Corvallis Environmental Research Laboratory, U.S. Environmental Protection Agency, 200 SW 35th St., and *Department of Zoology, Oregon State University, Corvallis, Oregon 97331.* Accepted for publication 18 April 1977.