

POSTNUPTIAL AND POSTJUVENAL MOLT IN WHITE-CROWNED SPARROWS IN CENTRAL ALASKA

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Breeding of migratory birds at high latitudes involves problems of allocation of time and energy among the functions of migration, reproduction itself, and molt. Indeed, in some species, notably swallows and flycatchers, the timing system that has evolved defers the postnuptial molt entirely or mainly until after the southward migration (Johnson 1963). In some populations or species, as in *Zonotrichia leucophrys gambelii* (Farner 1964), these three functions are sharply partitioned temporally through the course of the late spring and summer.

On the other hand, it is clear that the northernmost breeding populations of several species (e.g., *Fringilla coelebs*, *Phylloscopus trochilus*, *Parus major*) have evolved a solution involving a longer period of molt that overlaps the periods of reproduction, premigratory fattening, and southward migration (Blyumental 1965; Blyumental and Dolnik 1966; Blyumental and Zimin 1966; Blyumental et al. 1963; Dolnik 1967; Dolnik and Blyumental 1967). Despite the obvious importance of the timing of postnuptial and postjuvinal molts, information concerning their timing, rate, and patterns in migrant species is surprisingly meager and frequently lacking in detail. This hiatus is especially conspicuous in the crowned sparrows of the genus *Zonotrichia*, a group in which annual cycles have otherwise been studied thoroughly. We offer the following analysis of the summer molt of *Zonotrichia leucophrys gambelii* in central Alaska as a step toward illuminating these aspects of avian biology.

MATERIALS AND METHODS

We observed *Zonotrichia leucophrys gambelii* from 1 July through 3 September 1962 within a 10-mile radius around College (near Fairbanks), Alaska (64.8°N, 147.8°W), and examined 146 adults and 353 immatures that we shot or caught in mist nets. We made observations at many places near College, but collecting was concentrated in four areas: the University of Alaska Experimental Farm (on an alluvial flat about 140 m above sea level); the Dornath and Husak farms (on south-facing slopes at about 180–200 m) 5 miles and 5.5 miles, respectively, from College on Farmer's Loop Road; and at the Bushey farm (on a south-facing slope at about 280 m) 9.5 miles from College on the Steese Highway.

In addition to free-living White-crowned Sparrows, we studied 17 adults (8 females and 9 males) and one immature male captured on 5–7 July 1962 and kept in cages in an unheated room with natural daylight until 3 September. The housing and care of these birds have previously been described in detail (King et al. 1965). The plumage was examined at intervals of three or four days. Events in molt (e.g., dropping of feathers, first emergence of a pinfeather) that occurred between inspection days were estimated to the nearest calendar day.

In both captive and free-living birds the extent of postnuptial molt was recorded at each examination in terms of the number of rectrices and of primary and secondary remiges that were dropped, growing, or fully grown. A feather was regarded as "in growth" as long as blood was present in the calamus. The molt of body feathers was estimated as "light," "medium," or "heavy," and assigned numerical values of 1, 2, and 3, respectively. The progress and intensity of the postjuvinal molt were recorded by the same system (no flight feathers are replaced during the postjuvinal molt in *Z. l. gambelii*). The conventional American molt terminology is used uniformly. The primaries are numbered from proximal to distal, and the secondaries from distal to proximal, including the "tertials."

The schedule of work in both the field and the laboratory was so heavy that we did not have time to record the length of the growing flight feathers in

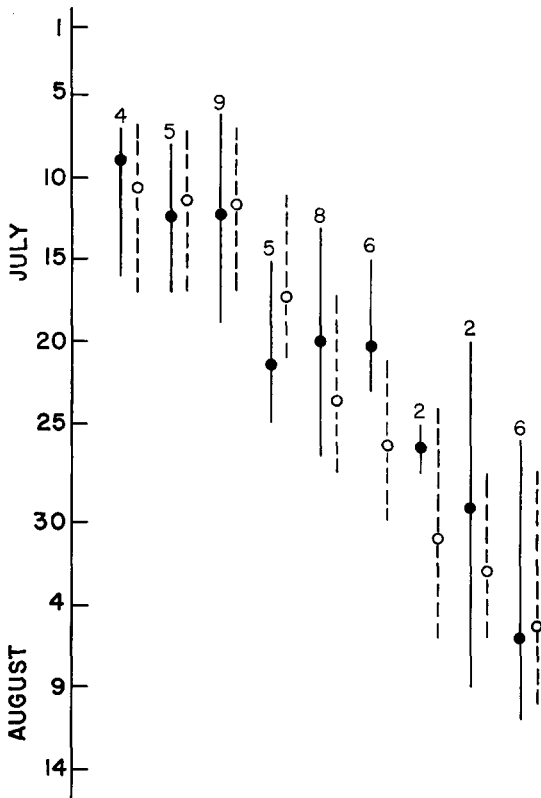


FIGURE 1. A comparison of time of molt in the primary remiges in captive (broken lines) and free-living (solid lines) White-crowned Sparrows at College, Alaska, in 1962. The vertical lines show the range of dates, and circles depict the means. The numerals at the top of the solid lines denote sample sizes for the free-living birds. For the captives, sample size is 17 in all cases. The data are arranged in order from P1 (left) through P9 (right).

a significant number of specimens. We are therefore not able to present our data in terms of "molt scores" that are directly comparable with those of systems currently in common use (e.g., Ashmole 1962; Evans 1966; Newton 1966; Foster 1967), but rely instead on other forms of analysis.

RESULTS AND DISCUSSION

POSTNUPTIAL MOLT

General chronology. The calendars of molt in captive and free-living White-crowned Spar-

rows are compared in table 1. Later in this report we will analyze more fully the molt in each category of plumage, but at this point we focus attention particularly on the close similarity of timing in the molt phases in captive and free-living birds. The chronology of molt was not significantly, if at all, altered by the conditions of captivity. Additional confirmation is obtained from a comparison of the progress of molt in the primaries (fig. 1). The general trends are alike in the two groups. Irregularities may be attributed mainly to the small samples in the free-living birds and to the fact that there were slight differences among sample sites with respect to the progress of the physiological cycles of the birds.

Because our captive White-crowned Sparrows clearly afforded a reliable sample of the postnuptial molt in the free-living population we have relied mainly on data obtained from the captives in the following analysis of the chronology and patterns of the molt.

Molt of the primaries. Ten adults examined in the field on 5-6 July had not yet begun to molt either body or flight feathers. The earliest molt of the first primary (P1) was noted in birds taken on 7 July. By extrapolation from the condition of the wing in specimens caught soon after this it is clear that a few birds in the region must have begun the molt of the remiges as early as 2 July, although the mean calculated date for the onset of molt in the captives was 7 July \pm 3.4 days (mean \pm sd; $n = 17$ in all cases unless otherwise indicated). Males and females did not differ significantly, statistically, in this or any other attribute of the postnuptial molt.

The first birds growing P9 were found in the free-living population on 26 July (fig. 1). The mean duration of the primary molt in individual captives was 37 \pm 3.4 days. The total span of primary molt in this group was 44 days. In the free-living populations that we sampled it was about 40 days.

The pattern of renewal of the primaries among the captives followed the expected sequence (Stresemann and Stresemann 1966:

TABLE 1. The calendar of molt in captive and free-living White-crowned Sparrows.

	Primaries		Secondaries		Rectrices		Body	
	Begin	End	Begin	End	Begin	End	Begin	End
Free-living birds								
(extreme dates)	2 July ^a	13 Aug.	20 July	20 Aug.	15 July	12 Aug.	5 July	23 Aug.
Captive birds								
(extreme dates)	2 July ^a	16 Aug.	22 July	23 Aug.	15 July	16 Aug.	1 July ^a	29 Aug.
(mean dates)	7 July	13 Aug.	24 July	18 Aug.	17 July	10 Aug.	8 July	25 Aug.

^a Extrapolated date

TABLE 2. Variation in the mean interval between first emergence of primary feathers during postnuptial molt in captive White-crowned Sparrows.

	Primary feather group		
	1-5	3-7	5-9
No. of birds	10	12	17
Span (in days) ($\bar{x} \pm sE^a$)	11.1 \pm 0.72	17.2 \pm 0.84	14.7 \pm 0.58
Mean interval between feathers (days)	2.76	4.29	3.68

^a Significance of differences: 1-5 vs. 3-7, and 1-5 vs. 5-9, $P < 0.01$; 3-7 vs. 5-9, $0.02 > P > 0.01$.

425) of regular progression from P1 through P9 in all cases. The tempo of replacement was not uniform through the series, but was slowest in the middle feathers (as suggested by the greater intervals between mean values in fig. 1). Our data are not adequate to allow a reliable evaluation of the interval between the emergence of each new feather and its predecessor in the series, but we can make a reasonable estimate of the average interval within groups (table 2). The pattern revealed here resembles that found in *Passer domesticus* by Zeidler (1966) and in *Corvus corax* by Gwinner (in Stresemann and Stresemann 1966: 35); the interval between emergences is shortest in the inner feathers, longest in the middle feathers, and intermediate in the outer feathers.

Within the group P1-P5 in the White-crowned Sparrow the shortest intervals are P1-P2 and P2-P3. The summary of means in figure 1 suggests that these intervals may be as short as one day or less. Our examination of individual birds confirms this. In several cases P1 to P3 were shed within the three-day interval between inspections. We cannot exclude the possibility that P1 and P2 or P1 through P3 are shed on the same day in some cases.

The total time-lapse between the emergence of P1 and P9 in individual captives averaged 25.8 days. In the remaining days of feather renewal in the primary series (11.3 days on the average) all primaries were growing simultaneously. The rate of feather growth cannot be uniform through the series. For instance, the length of the plucked P1 in a sample of seven male *Z. l. gambelii* that had just completed the postnuptial molt was 60.1 mm. This feather grows for an average of about 37 days, at a mean rate (which is probably not linear, but slows with time) of about 0.62 mm/day. In comparison, P9 averages 61.8 mm in total length and grows at a mean rate (11.3 days) of about 5.4 mm/day.

Molt of the secondaries. Newly emerging secondary remiges were first observed in free-living birds on 20 July (table 1). The mean date of onset in the captives was 26 July \pm 3.3 days. Growing secondaries were found in the captives during a span of 33 days. The mean duration of molt in the secondaries in individual birds was 25.7 \pm 3.3 days. Newly emerged secondaries were first detected most commonly when the emergence of the primaries had reached P6 (nine cases), and less commonly at P5 (six cases) and P7 (two cases). The sequence of molt through the secondary series was typical of passerine birds, with foci of initial growth at S1 and S7 or S8. In those cases among the captive birds in which the renewal of the secondaries was initially detected by the emergence of a single feather it was S8 in six cases, S7 in three cases, and S1 in one case. In the remaining seven birds it was not possible to ascertain accurately which of two or more growing secondaries had been the first to emerge.

The general pattern and relative intensity of the molt of the secondaries in the captive population is shown semi-schematically in figure 2. In this analysis all of the captives were arbitrarily set in phase with respect to the onset of the secondary molt, and the spread of values shown in figure 2 therefore results principally from individual variation in the times of emergence and rates of feather growth thereafter.

Unlike the growth of the primaries in the White-crowned Sparrows in our samples, the growth of some of the secondaries was completed while others were still elongating. On the average, the maximum number of secondaries that grew concurrently in an individual bird was 5.8. Typically there was a delay of about seven days between the emergence of S1 and the emergence of S2; and then S2-S6 tended to be renewed as a group. Our observations indicate that there is as little as one day

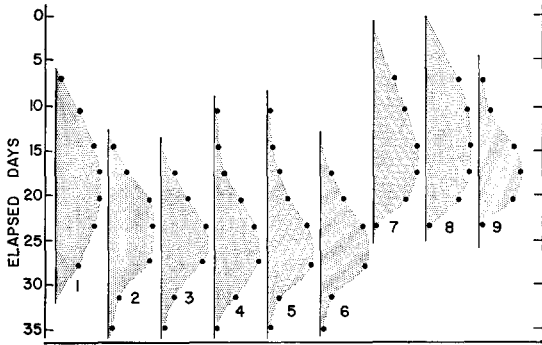


FIGURE 2. The pattern of molt in the secondary remiges in captive White-crowned Sparrows ($n = 17$) at College, Alaska, in 1962. All birds were placed arbitrarily in "day zero" on the day that molt of the secondaries began. The numeral beneath each curve denotes the feather number from S1 through S9. The peak of the curve for each feather represents the time at which the maximum number of feathers at that locus was in growth in the sample. For example, for S1, growth in the sample began on about day 6 after the onset of molt in the secondaries, reached a peak on days 17–21 (all birds growing S1), and decreased to no growth (growth ended) by about day 31.

between the shedding of successive feathers in this group, and it is possible that two or more feathers are shed simultaneously.

Molt of the rectrices. The earliest renewal of the tail feathers was found in both captive and free-living White-crowned Sparrows on 15 July (table 1). The mean date of onset in the captives was 17 July ± 2.2 days, and the period of growth to completion in individuals averaged 25.1 ± 5.3 days. Growing rectrices were found in the captives through a span of 33 days, and in the free-living populations through a span of 28 days. Renewal of the tail in the captives began most commonly when molt of the primaries had reached P5 (nine cases), but began in some as early as P3 (one case), P4 (five cases), and extended to P6 (two cases). The shedding of the rectrices was very rapid, often being completed in a three-day period between examinations, and leaving the bird briefly without a tail. Many specimens in a similar condition were caught in nets or seen in the field during this period. The completion of the growth of the new tail feathers was essentially simultaneous from R1 through R6.

Molt of the body feathers. The renewal of the contour plumage exclusive of the coverts began almost simultaneously with the shedding of P1 and extended beyond the end of the period of flight-feather growth (table 1). On the average, body molt in the captives began on 8 July ± 4.2 days and lasted for 49.2

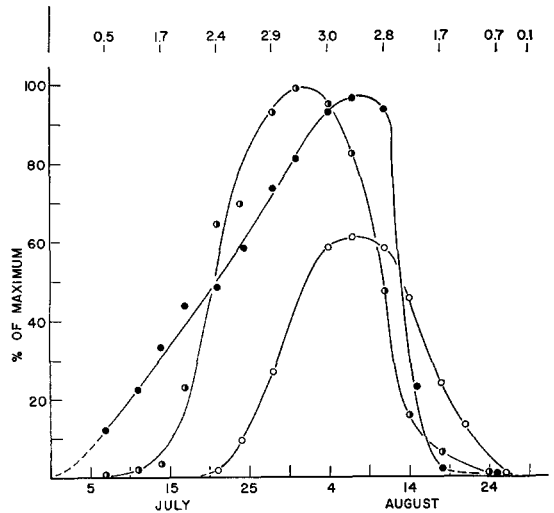


FIGURE 3. Phase relationships and relative intensity of molt in remiges (blackened circles = primaries; clear circles = secondaries), rectrices (half-blackened circles), and body feathers (line of numerals at top of panel) in captive White-crowned Sparrows at College, Alaska, in 1962. For the remiges and rectrices, 100 per cent of maximum molt indicates that all birds in the sample ($n = 17$) were growing all feathers in that category concurrently; 50 per cent indicates that half the feathers in that category were growing concurrently in the sample, and so on. The mean intensity of body-feather molt is shown on a scale from zero (no molt) to 3 (heavy molt).

± 5.2 days in individual birds. This last value is also the average duration of the complete postnuptial molt in individuals of the captive group. The peak of intensity in body molt was a broad one (see fig. 3) that coincided with the overlapping peaks of maximum growth in the flight feathers.

Integration of phases in the postnuptial molt. The phase relationships of molt in the different plumage categories are shown for the captive birds in figure 3. The calculations of relative molt intensity included all 17 birds, and the spread of values and the peaks of intensity therefore deviate slightly from the pattern for a single individual (for instance, in an individual the molt of primaries attains 100 per cent of possible number of primaries growing concurrently). Figure 3 represents the pattern of molt in a small and well-synchronized population.

It is evident that the peaks of molt intensity in all plumage categories substantially coincide. The algebraic sum of these curves is equivalent to the intensity of molt in all of the flight feathers, and reaches a sharp peak at 80 per cent on 5 August. This combined curve has been omitted from figure 3 in order to avoid undue complexity in the graph.

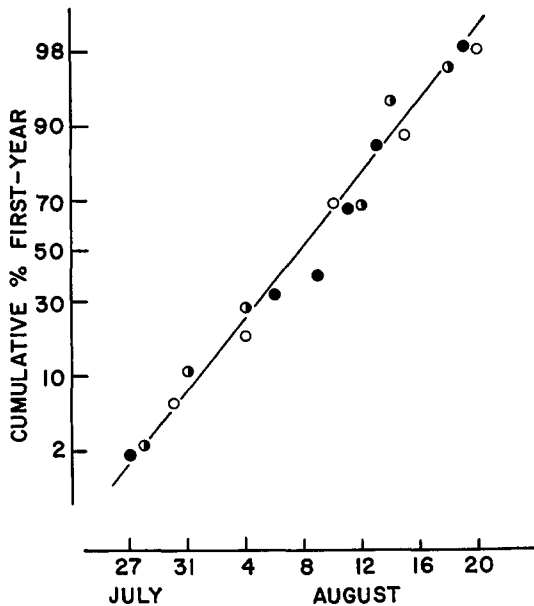


FIGURE 4. The time-course for the termination of postjuvénal molt in the regional population of White-crowned Sparrows, expressed in terms of cumulative percentages and depicted by the straight line. Data points are based on samples captured in 1962 at Bushey farm (clear circles), Dornath and Husak farms (blackened circles), and the Experimental Farm (half-blackened circles), sites near College, Alaska.

POSTJUVENAL MOLT

Postjuvénal molt was first detected in the free-living population on 5-6 July (two of nine birds examined). Only 4 of 82 immatures caught after 18 August were still molting (20, 22, 23, and 31 August). The last substantial numbers of molting immatures were caught on 18 August (five of nine were molting). It is therefore clear that the postjuvénal molt in the regional populations was essentially ended by 20 August. The postjuvénal molt in the population at large was thus accomplished almost entirely in the 46-day span of 5 July-20 August, which also delimits the maximum duration of postjuvénal molt in an individual bird. The minimum duration (from first observed postjuvénal molt to first complete first-year plumage) was 22 days. The median is 34 days, and is our best estimator for the duration of the molt in an individual.

Postjuvénal molt began in our single immature captive between 11 and 14 July and was completed between 14 and 18 August, thus requiring between 31 and 38 days. The single immature bird of the free-living population that we recaptured after banding had completed its postjuvénal molt in the 36-day period between 14 July and 18 August. On the basis of similar but more abundant data from re-

captured birds, DeWolfe (1967) estimated that the postjuvénal molt required an average of 33 days in individual White-crowned Sparrows near College, Alaska, in 1957.

The time-course of postjuvénal molt in our samples is conveniently displayed in terms of the cumulative percentage of the sample populations that had attained first-year plumage (completed the molt). The data are presented in figure 4. In this analysis we have combined the data from the adjacent Dornath and Husak sites in order to obtain a series of observations that spans the entire period of molt. It is clear from figure 4 that the completion of the postjuvénal molt is distributed in time approximately as a normal curve, thus yielding a straight line when plotted on a probability scale. The symmetry of this distribution suggests that there was no shortening of the period of postjuvénal molt as the season progressed. If the mean duration of the postjuvénal molt is 33 or 34 days, as our data and those of DeWolfe suggest, then it is evident from figure 4 that a small percentage (less than about two per cent) of the immatures must have begun the postjuvénal molt as early as 27 June. This is entirely possible. We did not begin to collect immature birds until 5 July, and our samples were small and confined to a single area.

RELATIONSHIPS OF SUMMER MOLT TO REPRODUCTION, POST-REPRODUCTIVE PERIOD, AND MIGRATION

We have previously shown (King et al. 1965), as has DeWolfe (1967), that reproductive capability and postnuptial molt are mutually exclusive in populations of White-crowned Sparrows near College, Alaska. Molt does not occur in either males or females until the gonads are regressing and approaching a minimum weight. Stresemann and Stresemann (1966) review the evidence that this is a common pattern among small songbirds of middle and high latitudes (see also Newton 1966).

The first evidence of the disintegration of family groups was recorded on 19-23 July in 1962, when flocks of 10-15 immatures were seen at several sites. By 30-31 July we were recording flocks of 60-70 birds. Flock-formation coincided with the termination of the postjuvénal molt (fig. 4). Adult birds remained conspicuously apart from the groups of immatures and were not seen with them until 5-7 August. After this time, which corresponded with the onset of the declining phase of postnuptial molt (fig. 3), flocks included both adult and immature birds.

During their molting period the adults

tended to remain in pairs and to show some territorial attachment (i.e., when chased they tended to move only short distances within a definable area), but song was uncommon and there was no evidence of territorial defense. The observations of DeWolfe (1967) of color-banded White-crowned Sparrows indicate that at least some adults do not remain on their breeding territories during the molting period. The weak "territorial" behavior that we observed may be merely a residue of reproductive territorialism and not rigidly centered on a stable site. Whether or not adult White-crowned Sparrows maintain "molting territories" is a subject that requires further investigation.

By 15–18 August, White-crowned Sparrows were absent from all of the sites except the Experimental Farm, where they had been abundant until this time. We assume that this disappearance, which coincided with the end of postjuvenile molt and the terminal stages of postnuptial molt, marked the onset of migration in the local population. White-crowned Sparrows were present at the Experimental Farm until 31 August, obviously attracted by the unusually abundant food supply there. Observations throughout our radius of operations revealed that the situation at the Experimental Farm was an artificial one that did not represent the region at large. The birds that we found there may have been transients from the north, or a premigratory gathering of local birds. Between 1 September and 3 September, when field work ended, the Experimental Farm, too, was empty of White-crowned Sparrows. It had snowed on 1 and 3 September.

Although our data from central Alaska in 1962 indicate that only a very small fraction of the population began migration while still molting body feathers, this observation should not be generalized to other years (see DeWolfe 1967) or to other populations. Among the hundreds of transient White-crowned Sparrows that we examine every year during the autumn migration in Washington, we commonly find a few individuals in light body molt as late as the end of September.

COMPARISONS WITH OTHER POPULATIONS AND SPECIES OF CROWNED SPARROWS

Mewaldt et al. (1968) studied populations of White-crowned Sparrows from the Pacific coast of North America. These included the southern nonmigratory form, *Z. l. nuttalli*; the northern short-range migrant, *Z. l. pugetensis*; and intergrades of these forms which occur in northern California. The onset of the post-

nuptial molt was recorded in samples of these populations kept in an aviary at San Jose, California (ca. 37.3°N latitude). *Z. l. nuttalli* from Pismo Beach, California (ca. 35°N), began the postnuptial molt between 20 and 27 May; *Z. l. pugetensis* from Sidney, British Columbia (ca. 49.5°N), began the molt between 3 and 10 June. There was no obvious orderly north-south progression through intermediate populations. Our sample of *Z. l. gambelii* at ca. 65°N began the postnuptial molt on about 2 July. The mean rate of latitudinal passage in the date of molt onset is therefore roughly one day of delay per degree of latitude northward between Pismo Beach and Sidney, and two days of delay per degree between Sidney and College, Alaska. We have no information on the duration of the postnuptial molt or on any aspect of the postjuvenile molt in the southern populations of *Z. leucophrys*.

Concerning the relationship between molting time and latitude, it can be calculated from data presented by Dolnik and Blyumental (1967) for three regional populations of the Chaffinch (*Fringilla coelebs*) that there is a delay of about 3.3 days per degree of latitude between Germany (50–54°N) and Karelia (62°N).

A detailed study by Miller (1961) of the molts of a nonmigratory form of the Rufous-collared (= Andean) Sparrow, *Zonotrichia capensis*, at ca. 3.2°N latitude in Colombia enables us to compare the molts of arctic and equatorial forms of *Zonotrichia*. The sequence of molts and plumages in *Z. capensis* differs from that in *Z. leucophrys* in lacking a pre-nuptial molt. This appears to be true in all of the many taxonomic forms of *Z. capensis* in Latin America (Chapman 1940). It is of interest in this connection that there is a north-to-south decrease in the intensity of the pre-nuptial molt in the North American forms of *Z. leucophrys* from which *Z. capensis* is presumably derived (Chapman 1940; Blanchard 1941; Banks 1964; Mewaldt et al. 1968). This resembles, at a different taxonomic level, the north-to-south decrease in the extent of pre-nuptial molt found by Foster (1967) in Orange-crowned Warblers (*Vermivora celata*) of the races *lutescens* and *orestera*.

Miller (1961) shows that individual adult *Z. capensis* undergo two complete molts in a 12-month period, each requiring about 40–80 days in different individuals, and averaging about 60 days. This may be compared with the average duration of 48 days in individual *Z. l. gambelii* studied in central Alaska. The

sequence and phasing of feather replacement in *Z. capensis* is similar to that of *Z. l. gambelii* in categories for which comparison is possible, except that body molt in *Z. capensis* is irregular in timing in relation to the growth of the primaries. Usually, the molt of the body feathers begins before the first primary is shed, but it is often delayed until after the onset of primary molt and in some instances did not begin until the emergence of P5 or P6. Body molt was usually completed by the time that the primaries were entirely renewed. In our samples of *Z. l. gambelii* we found that body molt usually began with or slightly after the shedding of P1 and extended significantly beyond the end of flight-feather growth.

Molt and reproductive capability were mutually exclusive in female *Z. capensis* but not in males, in which molt occurred at all levels of testicular development.

The postjuvinal molt of *Z. capensis* usually involves only the body feathers, but in some cases (estimated by Miller at no more than 10–15 per cent of the population) involved also secondaries 7, 8, and 9, and their coverts, and the rectrices (estimated at 25–30 per cent of the population). We have no evidence that these or any other flight feathers are ever replaced during the postjuvinal molt in *Z. leucophrys*. *Z. capensis* also differs from the northern forms in that an adult plumage is acquired during the postjuvinal molt, without an intermediate first-year stage.

Postjuvinal molt in individual *Z. capensis* in Colombia lasts 50–100 days, but is most commonly completed in about 70 days (Miller 1961). This may be compared with an average duration of 34 days in *Z. l. gambelii* in central Alaska.

Miller (1961) found molting *Z. capensis* throughout the year in Colombia, although the adult molts were concentrated in broad peaks centered in February through April and late July through October (the principal nonreproductive seasons).

The general attributes of molt in *Z. capensis* compared with *Z. l. gambelii* include its slow tempo, great variability in duration among individuals, and great variability of timing within the population. Obviously this leisurely pace and labile relationship with seasonal progression is not tolerable in migratory forms that breed in the strongly periodic northern latitudes.

COMPARISONS WITH OTHER SPECIES OF MIGRATORY SONGBIRDS

We do not propose to review here the extensive literature concerning the patterns and

temporal characteristics of molt in small songbirds. It is not possible for us to improve on the analysis of these subjects provided by Stresemann and Stresemann (1966), except to take note of a few reports published subsequently. However, some comparisons of the summer molt of *Z. l. gambelii* with the molt of other species are useful in order to illuminate common patterns and noteworthy adaptations.

Detailed information on the summer molt of migratory songbirds at high latitudes is surprisingly sparse. Stresemann and Stresemann (1966) note that the postnuptial molt of the Snow Bunting (*Plectrophenax nivalis*), the Lapland Longspur (*Calcarius lapponicus*), and some similar species of the Arctic requires an estimated 30–40 days, or somewhat less than the 48 days required for the postnuptial molt in *Z. l. gambelii* in our Alaskan samples. In a particularly thorough study of the molt of the Lesser Redpoll (*Carduelis flammea cabaret*) in central England at ca. 55°N, Evans (1966) found that the postnuptial molt required about 56 days in individuals, with no difference between the sexes. In northern Norway at 70°N the duration of postnuptial molt in this species was about 48 days in males and about 54 days in females (Evans et al. 1967).

Salomonsen (1950:531) notes that the flying ability of Lapland Longspurs in Greenland is seriously impaired during the postnuptial molt, and Berger (1967) reports a similar situation in the Thrush Nightingale (*Luscinia luscinia*) studied at Hiddensee (ca. 54.5°N). This species requires only 30–35 days to renew the plumage in the postnuptial molt. Berger reports that all rectrices and up to six primaries may grow concurrently, and that in one specimen P2 to P8 were growing at the same time and only P1 was entirely cornified. Similarly, Stone (1896) found seven primaries growing concurrently in two Snow Buntings from Greenland.

Compared with the pattern in *Z. l. gambelii*, the intensity of the postnuptial molt in these species is not at all extraordinary. All nine primaries, all of the rectrices, and an average of about six secondaries grow concurrently during the postnuptial molt in the typical White-crowned Sparrow in central Alaska. Nevertheless, we have never observed any instance of seriously impaired flying ability in any of the hundreds of adults that we have observed in the field during the time of the postnuptial molt. We are not able to explain the basis of this maintenance of flight efficiency during a molt that is ostensibly more intense, at least

in terms of the number of flight feathers involved, than it is in species that are reportedly rendered essentially flightless during at least part of the molt. It seems obvious that there must be some adaptive correlation between the frequency of ecdysis and the rates of feather growth which serves to maintain the aerodynamic qualities of the wing during molt in the White-crowned Sparrow. Our data are not adequate to permit an examination of the growth patterns that might make this possible, and the resolution of the question must await further investigation.

The postjuvinal molt in White-crowned Sparrows in central Alaska requires about 34 days in an individual bird. Immature Chaffinches near the shore of the Baltic Sea at about 55°N require about 42 days to complete the postjuvinal molt if it begins early in the summer (birds of early nestings), and a progressively shorter period down to a minimum of about 38 days later in the summer (Dolnik and Blyumental 1967). A similar decrease in the duration of postjuvinal molt (or the age at which the molt is complete) through the summer has been reported for *Passer domesticus* by Zeidler (1966) and for *P. m. montanus* by Deckert (1962). We have no information on this subject for White-crowned Sparrows in central Alaska. Because the reproductive period is very short (see King et al. 1966; DeWolfe 1967) and there is little variability around the mean time of hatching and of postjuvinal molt in the populations in central Alaska, there is, in any case, very little range for an adaptive shortening of the molt through the season. The sequence of events in the summer season is already fully compressed in this population.

An interesting, although speculative, inference can be drawn with respect to differences between *Zonotrichia leucophrys gambelii* and *Fringilla coelebs* in their adaptations of the postnuptial molt schedule to conditions at high latitudes. In the latter species in Karelia (62°N), the postnuptial molt of the remiges requires at least 75 days. Although this is a somewhat shorter and more intense molt than in more southern populations (Blyumental et al. 1963; Blyumental 1965; Dolnik and Blyumental 1967), it nevertheless begins during the period of feeding of the young and extends well into the migratory period (Blyumental 1965; Dolnik 1967). In contrast, in *Z. l. gambelii* (table 1) at a comparable latitude the molt of the remiges requires only about 40 days and is restricted to the period between the end of reproductive activity and

the beginning of migration; the entire postnuptial molt requires about 48 days, with the body molt extending only to a minor extent into the migratory period and in only a small fraction of the population. Thus, in adapting to higher latitudes, the Chaffinch appears to have employed a strategy of retaining a protracted molting scheme with a relatively low daily energy cost that is compatible with an overlap with the energy expenditures of feeding young and of migration. The overlap with feeding of the young, and the intensification of molt in comparison with more southern populations, may be compensated by the longer days available for feeding. Possibly the overlap with migration can be explained by the daytime migration of this species. Unfortunately, comparative data on the rates of migration of *F. coelebs* and *Z. l. gambelii* do not exist. The strategy in *Z. l. gambelii*, in contrast, has emphasized a sharp partitioning of time and energy for reproduction, postnuptial molt, and fall migration. This may well have involved an intensification of molt and a shortening of the molting period, but this suggestion cannot be examined critically until adequate data are available from more southern breeding populations of this species.

SUMMARY

The phenology of the postnuptial and postjuvinal molts in the White-crowned Sparrow was ascertained from examination of 500 free-living birds near Fairbanks, Alaska, during 1962. At the same time, the pattern of postnuptial molt was studied in 17 captive adults exposed to natural temperature and photoperiod. There were no conspicuous differences between free-living and captive birds, and the data from these groups were combined in the general analysis.

Postnuptial molt began in the population in the first week of July and ended by 25 August. In individual birds, the complete postnuptial molt required about 48 days. Renewal of the primary remiges required 37 days in the average individual; all nine primaries grew concurrently during the last 11 days of this period. Renewal of the secondary remiges required 26 days in the average individual, and a maximum of six secondaries grew concurrently. The renewal of the rectrices required about 25 days, all 12 growing concurrently. Molt of the contour plumage usually began with the shedding of the first primary and continued for about one week after the completion of growth in the flight feathers.

Postjuvinal molt began in the population in

the last few days of June and was essentially ended by 20 August. The duration of molt in an individual bird was about 34 days.

Midsummer flock-formation began in immature White-crowned Sparrows in the third week of July, when the postjuvenile molt was well advanced. Adults initially remained apart, but began to join the immatures in flocks in the first week of August during the declining phase of the postnuptial molt. Migration, or premigratory gathering, of the local population began soon after 15 August, and White-crowned Sparrows were absent from the region after 1 September. A few of them must have begun the southward movement before body molt was finished.

The summer molt of White-crowned Sparrows in central Alaska is characterized by its brevity, intensity of flight-feather growth, and conspicuous precision in timing within the population. At present these attributes appear to be quantitatively unique, although future studies of small migrant songbirds at high latitudes may reveal that they are part of a common pattern of adaptation.

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