

POSTNUPTIAL MOLT AND ITS RELATION TO REPRODUCTIVE CYCLE AND BODY WEIGHT IN MOUNTAIN WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS ORIANTHA*)

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The body of information available on the relationship of postnuptial molt to reproductive functions indicates that, in general, these events are separated in time in birds that have altricial young. This is true of those that live in the tropics as well as the temperate zone, regardless of whether they are migratory or nonmigratory (Miller 1961, 1963; King et al. 1965; Moreau 1966; Newton 1966; Stresemann and Stresemann 1966, 1968; Morton et al. 1969; Payne 1969a; Wolf 1969). Apparently the energetic costs of feeding young prohibit all but the most protracted types of molt during this period.

The postbreeding migration and the metabolic preparation for it would seem to impose further rather important restrictions on the phenology of molt in migratory species or populations. Apparently, however, nearly all permutations of overlap between molt, pre-migratory fattening, and migration exist (Blyumental 1961; Blyumental et al. 1966; Dolnik 1967; Dolnik and Blyumental 1967; Stresemann and Stresemann 1968, 1969). Most of the more complete natural history studies have been confined to those species wherein molt is relatively protracted, and little is known about the way that energy is allocated among these functions in birds that have a brief but intense postnuptial molt. This type of molt is probably most prevalent in migrants that breed at high latitude or high altitude, environments that often are suitable for occupancy for only 3.5 to 4 months per year.

Herein we present details on the timing and pattern of postnuptial molt and their relationship to aspects of reproduction and pre-migratory fattening in *Zonotrichia leucophrys oriantha*. This race of White-crowned Sparrow winters in the lowlands of the southwestern United States and northern México and

breeds in high altitude meadows of the western United States.

MATERIALS AND METHODS

This study was conducted throughout the summers of 1968–70 near Tioga Pass, Mono County, California. The subalpine meadows in this area between altitudes of 2896 and 3048 m were utilized as breeding habitat by *Z. l. oriantha*.

Birds were captured with mist nets or live traps. Body weights were measured to the nearest 0.1 g on a pan balance. The condition of molt was recorded and the length of all flight feathers renewed on the left wing and left half of the tail was measured with a millimeter ruler. Sex was determined by laparotomy or, when present, by a brood patch or cloacal protuberance. All released birds were fitted with Fish and Wildlife Service bands. In addition, a red plastic band was placed on females and a blue band on males above their service bands. This allowed us to determine sex during our close-up behavioral observations.

A total of 138 adult males yielding 360 recaptures and 107 adult females yielding 174 recaptures was processed.

In early July of 1969 and 1970, a group of adults was placed in captivity until late September. They were held two per cage in 30 × 21 × 20 cm cages in a 4.5 × 4.5 m tent with mesh windows or doorways on all sides. Thus, they were exposed to natural oscillations of temperature and photoperiod. Commercial game bird mix and mixed seeds plus water in bottles were always provided. The captives were weighed and examined for condition of molt three times per week in the early afternoon.

Winglengths were measured on hand-held live birds from the bend of the wing to the tip of the longest remex. Our measurements of *Z. l. gambelii* were taken from a population that winters in the Owens Valley, Inyo County, California.

RESULTS AND DISCUSSION

THE CHRONOLOGY OF MOLT

Postnuptial molt began in late July or early August in wild and captive birds throughout the study period (table 1). In wild birds molt began earliest in 1968. This was related to the early snow melt and appearance of dry conditions that caused relatively early termination of reproduction (Morton et al. 1972).

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TABLE 1. Date for beginning of postnuptial molt in *Zonotrichia leucophrys oriantha*.

Year	Sex	N	Mean ± S.D. (Days)	Range
Wild Birds				
1968	Males	31	23 July ± 10.9	15 July- 4 Aug
	Females	9	25 July ± 6.8	16 July-14 Aug
	Combined	40	24 July ± 7.8	15 July-14 Aug
1969	Males	27	2 Aug ± 5.5	21 July-15 Aug
	Females	16	3 Aug ± 9.9	20 July-21 Aug
	Combined	43	2 Aug ± 10.4	20 July-21 Aug
1970	Males	21	1 Aug ± 6.4	20 July-11 Aug
	Females	20	6 Aug ± 11.3	19 July-24 Aug
	Combined	41	3 Aug ± 9.4	19 July-24 Aug
Captive Birds				
1969	Males	10	1 Aug ± 4.4	26 July- 8 Aug
	Females	10	2 Aug ± 7.9	28 July- 7 Aug
	Combined	20	2 Aug ± 4.1	26 July- 8 Aug
1970	Males	9	30 July ± 6.2	22 July-11 Aug
	Females	11	28 July ± 6.6	17 July- 7 Aug
	Combined	20	29 July ± 6.3	17 July-11 Aug

Also, in the wild population molt began slightly earlier in males each year than in females. We are convinced that this difference is meaningful and that it is due to a temporal separation of two natural events that evidently are energetically incompatible: molt and the feeding of young. This becomes clear when one compares the onset of molt in known pairs. In the course of the study, we were able to determine the day when postnuptial molt began for both members of nine pairs. We do not know precisely the relationship between the termination of feeding young and the onset of molt in these pairs, but we do know that molt began in males an average of 19.5 ± 9.1 days after their broods had hatched. In females, the interval was 27.6 ± 8.9 days. Thus, molt began an average of 8.1 days earlier in the males than in females. The delay between hatching of young and the onset of molt corresponds closely to the interval that we have observed the young being fed by color-banded adults (Morton et al. 1972). We have, however, observed several times adults in the first stages of molt still feeding fledglings. The most extreme case was a female feeding young 14 days of age when her molt began. It has been reported in another high altitude breeder, the Water Pipit (*Anthus spinoletta*), that the male begins molting 2 weeks ahead of the female and while they are still feeding nestlings (Verbeek 1970).

In captive birds, molt began at about the same time as in wild birds, but males did not necessarily molt ahead of females (table 1). This is understandable since these birds were not engaged in reproductive activities.

MOLT IN MAJOR FEATHER GROUPS

Flight feathers. The onset of postnuptial molt was signaled in every case by the loss of the first primary (P_1). In 38.7% of the cases P_2 was dropped on the same day as P_1 , and in 3.2% of the cases P_1 - P_3 were dropped together. The loss of primaries proceeded regularly from P_1 to P_9 , but it did not proceed uniformly over time (fig. 1). Following the loss of P_1 , P_{2-4} were dropped at an average interval of 1.5 days between feathers. The interval for P_{5-7} was 4.8 days, and for P_{8-9} it was 1.9 days. This pattern whereby the central primaries are lost at a slower rate than the terminal ones was observed in *Z. l. gambelii* (Morton et al. 1969) and has been noted in other passerines (Stresemann and Stresemann 1966). On the average, primaries were growing for 46.1 days.

The molt of secondaries always began in an individual with S_8 , then usually in the sequence of S_7 , S_9 , S_1 , S_6 , and S_{3-5} . The average time span over which secondaries were growing was 38.3 days.

This pattern wherein the three innermost secondaries or tertiaries are molted ahead of the other secondaries is the usual sequence in passerines. The focus at S_8 was also seen in *Z. l. gambelii* in the postnuptial molt (Morton et al. 1969) and in the prenuptial molt (Michener and Michener 1943). The loss of S_6 ahead of S_{3-5} occurred 53.6% of the time, and indicates a possible affinity between it and S_{7-9} . Molt in the rectrices proceeded regularly from R_1 through R_6 . R_2 was shed an average of 2.9 days after R_1 and R_{2-6} were then dropped within the subsequent 5.5 days.

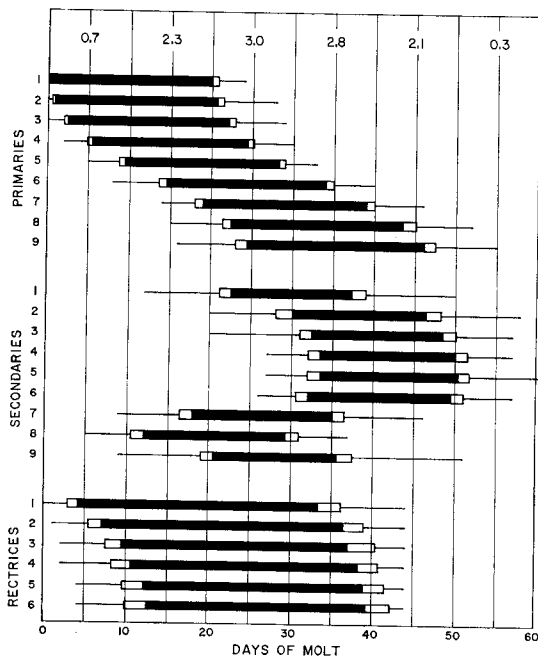


FIGURE 1. Chronology of flight-feather molt in *Zonotrichia leucophrys oriantha*. Black bar shows mean onset and termination of growth, white bar shows 2 S.E., and horizontal line shows range for growth in individual feathers. All data are set in relation to time P_1 was shed. $N = 30$. Numerals at top indicate intensity of body-feather molt (see text).

Rectrices were in growth for an average of 35.1 days:

Body feathers. The replacement of body feathers began in most birds, to the best of our knowledge, on the day P_1 was dropped or very shortly thereafter. We usually detected it first in the cervical region of the spinal tract. In most cases, body feathers continued to grow for a few days beyond the end of flight-feather growth. Thus, the duration of body-feather replacement delimits the total duration of postnuptial molt.

A numerical estimate of the intensity of body-feather molt in relation to the course of flight-feather molt can be seen at the top of figure 1. The numerical rating was derived from subjective estimates of no, light, medium, or heavy body molt being given scores

TABLE 2. A comparison of the average duration of molt in days in feather groups of two races of *Zonotrichia leucophrys*.

	Feather groups			
	Primaries	Secondaries	Rectrices	Body
<i>Z. l. gambelii</i> ^a	37.0	25.7	25.1	49.2
<i>Z. l. oriantha</i>	46.1	38.3	35.1	48.8

^a Data taken from Morton et al. (1969).

TABLE 3. Winglength in millimeters of *Zonotrichia leucophrys*.

	Sex	N	Mean	S.D.
<i>Z. l. gambelii</i>	Male	114	79.82	1.91
	Female	87	75.40	1.87
<i>Z. l. oriantha</i>	Male	55	82.98	1.90
	Female	54	77.37	2.18

of 0, 1, 2, or 3, respectively. Thus, for example, on Day 25 of molt all birds were in heavy body molt and the maximum mean score of 3.0 was obtained.

DURATION OF MOLT

In 14 captive females, the mean duration of molt was 48.0 ± 4.0 days. In 16 males, it was 49.6 ± 6.2 days. This difference is not statistically significant ($P > 0.4$). For the 30 birds combined, the mean duration of molt was 48.8 ± 5.2 days. Our notes on retrapped wild individuals suggest that this datum from captives accurately indicates the duration of molt in wild birds. Extending data on molt from captives to the wild population has been shown previously to be a valid technique, at least for some species (Morton et al. 1969; Newton 1969).

The duration of postnuptial molt (body-feather molt) in *Z. l. oriantha* is apparently the same as that found in *Z. l. gambelii*. Seventeen adult *Z. l. gambelii* held captive at their breeding area in Alaska molted for a period of 49.2 ± 5.2 days (Morton et al. 1969).

There is considerable difference in the sequence and duration of flight-feather molt in the two races of migratory *Zonotrichia leucophrys* that have now been studied on their breeding grounds. In *Z. l. gambelii*, each group of flight feathers is in growth for a shorter period than in *Z. l. oriantha* (table 2). The growth of body feathers, however, occurs for about the same length of time.

It should be mentioned that *Z. l. oriantha* is slightly larger than *Z. l. gambelii*. This is evident in museum skins measured by Banks (1964), by our measurements of winglength (table 3), and in body weights of live birds (see beyond).

MOLT IN RELATION TO REPRODUCTIVE CYCLE AND BODY WEIGHT

During our three summers of routine handling of banded adults, we compiled many records on individuals with known histories. Using the chronology of molt established with

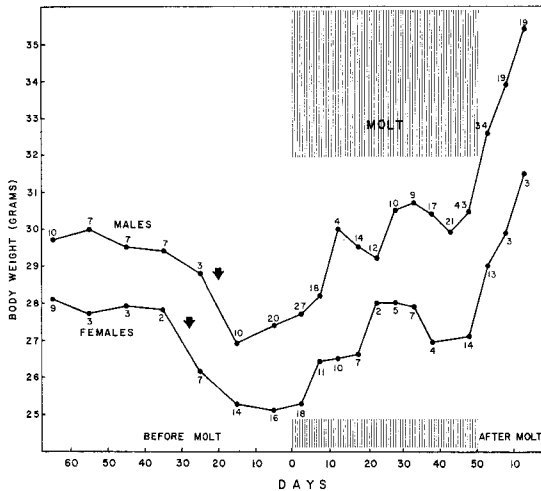


FIGURE 2. Mean body weights in *Zonotrichia leucophrys oriantha* in relation to postnuptial molt. Numerals indicate sample size. Arrows denote mean time when broods hatched in relation to beginning of molt.

captives in conjunction with our detailed notes taken on molt in these recaptured wild birds, we established accurately the onset of postnuptial molt in 37 females and 72 males. Taking the first day of molt in these individuals as a common point in their annual cycle, we can define their period of molt in relation to their body weights and reproductive activities (fig. 2).

Males lost weight for a short time after the chicks hatched but then began gaining. A general upward trend in body weight occurred throughout the period of molt. Females lost body weight right up to the time they began molting, then they too showed a tendency to gain weight during molt. Our observations indicate that the attentiveness of males is limited mostly to the nestlings, a period of about 10 days, whereas females continue to feed chicks for 2–3 weeks after they have fledged. Thus, the energy demands of rearing young and the unequal roles played by the adults in this process have discernible effects on body weights and the timing of postnuptial molt.

At the end of molt an additional, very rapid increase in weight occurred in both sexes. This was a final phase of metabolic preparation for migration that was terminated when these birds, now fat, left the breeding grounds.

An interesting comparison can be made of the energetic strategies employed by two migratory races of *Zonotrichia leucophrys*. Despite the variation in duration of molt in the various groups of flight feathers (table 2), the rate at which remex molt is accomplished

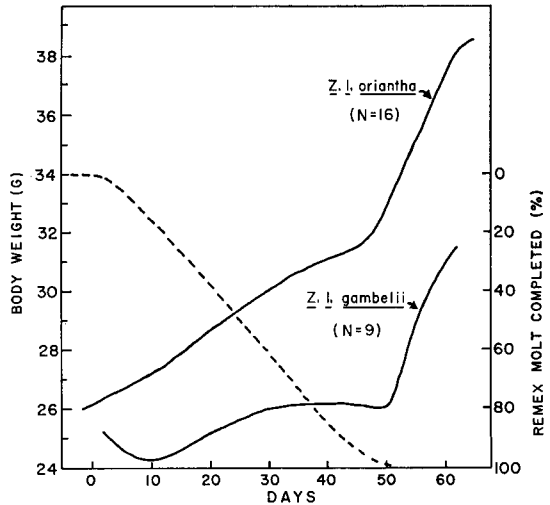


FIGURE 3. Body weights (solid lines) in relation to schedule of postnuptial molt (dashed line) in captive *Zonotrichia leucophrys* males. Data on *Z. l. gambelii* taken from King et al. (1965) and Morton et al. (1969).

is very regular and, as near as we can determine, nearly identical in both races. Therefore, we have constructed a curve that depicts accurately the chronology of remex molt for both *Z. l. oriantha* and *Z. l. gambelii* (fig. 3). In relation to this common denominator, we have shown the seasonal change in body weights as obtained from captive males.

There was a slight oscillation in body weight in *Z. l. gambelii* during the first weeks of molt. Weights were then stable until the end of molt at which time they began to increase rapidly as the birds deposited fat. The ether-extractable lipids of these birds at the end of the experiment amounted to 21.3% of total body weight (King et al. 1965). In contrast, *Z. l. oriantha* gained weight steadily throughout the period of molt. They showed also a phase of rapid gain that began as molt ended. The total ether-extractable lipids of these birds at the end amounted to 26.7% of body weight.

Others have documented slight increases in body weight during molt that have been attributed to an increase in lean dry weight, fat, or water content (King et al. 1965; Evans 1966; Newton 1968; Blackmore 1969; Payne 1969b; Myrcha and Pinowski 1970). The maximum increase detected was about 15%. The increase seen in *Z. l. oriantha* was about 23% and we are confident that it was due mostly to fat accumulation. This contention is supported by our observations of visible fat stores in these birds.

Very probably the final, rapid phase of

fattening in both groups shown in figure 3 was the result of an increase in food consumption. In the case of *Z. l. oriantha*, however, hyperphagia obviously began early in the period of molt. Did their final increase in rate of weight gain represent an additional increase in appetite or was it due to a shift in energy from feather growth to fat accumulation?

The energetic cost of molt has been determined for many species but in all examples that we can find, molt occurs at a more leisurely pace than in *Z. l. oriantha*. In the House Sparrow (*Passer domesticus*), theoretical and empirical values for the daily cost of molt are in close agreement and are on the order of 1.5–2.0 Kcal/day (King and Farner 1961; Blackmore 1969). However, costs may range as high as 5.5 Kcal/day depending on the stage of molt and environmental conditions.

Postnuptial molt takes about twice as long in *P. domesticus* as it does in *Z. l. oriantha*, but these birds are about the same body size. If we assume that the total cost of feather replacement is the same for both species then, during molt, *Z. l. oriantha* divert about 3.5 Kcal/day toward feather growth. Following the completion of molt, their increase in rate of weight gain was about 0.55 g/day. Thus, stored reserves were increased by 4.7 Kcal/day if one assumes that 90% of the weight increase was fat (McGreal and Farner 1956) and that the heat of combustion of fat is 9.45 Kcal/g (Brody 1945:35). It seems probable that a further increase in food intake occurs in *Z. l. oriantha* at the end of molt.

This amount of fattening during postnuptial molt is unusual and may be both permitted and necessary in birds breeding at high altitudes. We suggest that the response is permitted by an abundant food supply present in this environment during the summer. It may be necessary because fat accumulated well in advance of normal migration would allow vertical movements to milder conditions at lower altitudes in the advent of early autumnal storms. More information is needed, however, before we can generalize with confidence about the patterns of adaptation in high-altitude breeders.

SUMMARY

The timing and progress of postnuptial molt was measured in wild and captive *Zonotrichia leucophrys oriantha* on their central Sierra Nevada breeding ground. Molt began with the loss of the first primary and with contour feathers of the dorsal cervical region. The

replacement of new flight feathers proceeded regularly and their total daily increment of growth was nearly constant. The period of feather renewal lasted for an average of 48.8 days.

Evidently the feeding of young and postnuptial molt are incompatible events energetically because they seldom occurred simultaneously in a given adult. The nonoverlap of these events affected the onset of molt in mated pairs in that females fed fledglings for a longer period than males and molt began in them about 8 days later than in males. The chronology of molt for the population was also affected by reproductive activities. Molt began about a week earlier in 1968, a dry year, than in 1969 and 1970, wet years more suitable for a prolonged period of reproduction.

Due to fat accumulation, body weight increased by about 25% between the end of reproduction and migration. Fattening and molt were compatible energetically in that about half of the total weight gain occurred during the period of molt and half immediately following the completion of molt.

Compared to a previously studied migratory conspecific, *Z. l. gambelii*, feather growth proceeded more slowly in *Z. l. oriantha* in the major categories of flight feathers, but the total duration of postnuptial molt was the same. Different metabolic preparations for autumnal migration are employed by these races in that *Z. l. gambelii* fattens after molt is completed and *Z. l. oriantha* fattens both during and after molt.

ACKNOWLEDGMENTS

We wish to thank Cynthia Carey, Judith Horstmann, Jorge Orejuela, and Janet Osborn for assistance in the field. Robert B. Payne made helpful criticism of the manuscript and graciously let us read his unpublished review on the mechanisms and control of molt. Financial support was provided by the American Philosophical Society and by COSIP Grant GY-4754 to Occidental College from the National Science Foundation.

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Accepted for publication 31 January 1972.