



## DYNAMICS OF POSTNUPTIAL MOLT IN FREE-LIVING MOUNTAIN WHITE-CROWNED SPARROWS<sup>1</sup>

GALEN A. MORTON<sup>2</sup> AND MARTIN L. MORTON<sup>3</sup>  
*Department of Biology, Occidental College, Los Angeles, CA 90041*

**Abstract.** Data were collected on postnuptial molt by frequent measurements of primaries during eight consecutive seasons on *Zonotrichia leucophrys oriantha* of known sex, age, and reproductive history. Molt onset, marked by the shedding of P<sub>1</sub>, had a mean date that varied interannually by 17 days for both sexes and occurred earlier in males than in females in all years of the study. Molt duration of males regularly exceeded that of females and was greater by 2.7 days when all data were considered. Males were consistently trapped more often than females throughout the 7-week period of molt with captures being fewest for both sexes during Weeks 3-5. Duration of molt was unaffected by age in either sex but onset of molt occurred earlier in yearling males (many of which were unpaired) than in older males. Molt duration was fairly constant in both sexes regardless of molt onset but it was notably longer in the earliest group of males to begin molt and shorter in the latest group of females. Ovaries were invariably regressed with small follicles at onset of molt although brood patches ranged from being regressed to fully functional. Testis and cloacal protuberance lengths were variable at molt onset, tending to be about midrange in size but ranging from near seasonal maxima to minima.

Cessation of reproduction (indexed by laying date of a pair's last egg of the season) was followed more closely by onset of molt as the season progressed. Eventually the interval between these functions decreased by about 30 days in females and 40 days in males. In birds that nested latest in the season, molt sometimes began when they still had eggs. In fact, induction of molt was found to occur at all stages of the nesting cycle, leading at times to extensive overlapping of molting and reproductive activities. At least some overlap occurred in about three-fourths of the birds because that fraction went into molt before fledglings achieved independence.

Comparisons were made of molt and body mass dynamics and of reproductive success in two cohorts, one that began molting with nestlings or earlier (Group 1) and the other with fledglings or later (Group 2). Responses of males and females were dissimilar. Neither molt onset date nor its duration were different in males of the two groups although some individuals in Group 1 did show a marked delay in shedding P<sub>2</sub> and P<sub>3</sub>. Group 1 males were heavier through molt than Group 2 males. In contrast, molt onset date was also unaffected in females but its duration was about 3 days longer in Group 1. The P<sub>2</sub>-P<sub>3</sub> shedding delay occurred consistently in Group 1 females resulting in a decrease in the number of primaries growing simultaneously during the second week of molt. Later, after fledglings were independent, molt was accelerated in Group 1 females, not because shedding intervals decreased, but because growth rates increased in P<sub>3</sub>-P<sub>9</sub>. Unlike males, body masses of females tended to be lower in members of Group 1 until the final weeks of molt. We attribute these sexual differences to changes in energy demands caused by altered parental roles. Group 1 males provided less care than those in Group 2. Thus, temporal overlap of molt with reproductive functions was minimized in Group 1 males and maximized in their mates. This shift to uniparental care resulted in a decrease in the proportion of nests fledging young and in the number of chicks fledged per nest by Group 1 birds.

<sup>1</sup> Received 17 February 1990. Final acceptance 31 July 1990.

<sup>2</sup> Present address: Jefferson Medical College, Philadelphia, PA 19107.

<sup>3</sup> Corresponding author.

We suggest that this situation exists because migratory birds summering at high altitude try to breed for as long as possible but they must also complete their molt and become able fliers before the advent of winter conditions. The interactions of these opposing forces has led to selection for a control mechanism that schedules molt independently from the termination of reproduction.

*Key words:* Molt breeding overlap; postnuptial molt; reproductive success; migration; *Zonotrichia leucophrys*; White-crowned Sparrow; high altitude; montane.

## INTRODUCTION

Reproductive efforts and postnuptial molt are usually mutually exclusive events in the annual cycle of migratory passerines (Farner et al. 1980, Farner 1983). The logic has often been advanced that energetic demands are responsible for this temporal separation (Kendeigh 1949) and that reproductive and molting schedules probably have closely coupled control systems with at least part of the linkage between them being exerted by gonadal steroids because these are known to have an inhibitory effect on molt onset (see reviews by Payne 1972, Farner 1983). This line of reasoning is supported by recent field endocrine studies showing that gonadal steroid levels are minimal during the molting period (Wingfield and Farner 1977, 1978a, 1978b; Morton et al. 1990), and that molt onset can be delayed by steroid implants in free-living individuals (Runfeldt and Wingfield 1985, Schleussner et al. 1985). Thus expression of molt would normally be expected to follow gonadal involution and its accompanying decrease in hormone production. There is some warranted skepticism about the general applicability of these hypotheses, however, because there is a long-standing data base which shows that reproductive efforts and molt are not always mutually exclusive (Selander 1958, Miller 1961) especially in tropical species with long breeding seasons (Miller 1961; Payne 1969, 1972; Foster 1975; Thompson 1988). Nor are the two cycles obligately coupled, as illustrated in captives held long-term under 12L:12D that exhibited testicular cycles but did not molt (Farner et al. 1980). Temporal overlap between parental care and molt has now been noted in a wide array of temperate species (Bancroft and Woolfenden 1982, Zaias and Breitwisch 1990) including several that breed at high latitude (Pitelka 1958, Jehl 1968, Orell and Ojanen 1980) and high altitude (Verbeek 1970, Morton and Welton 1973). Understanding how molt is controlled in these various situations is inherently problematic because interspecific differences, presumably a result of differing selective pres-

ures, may have led to entirely different control mechanisms (Mewaldt and King 1978, Moore et al. 1982, Farner 1983). Therefore, a single descriptive pattern, applicable to all species, probably does not exist (Stresemann and Stresemann 1966, Payne 1972, King 1974). In addition, for a number of practical reasons, many of the functional realities of the reproduction-molt relationship in natural populations have not yet been laid bare. Molt dynamics are difficult to document in free-living individuals because frequent recaptures over a span of many weeks are required and just at the time when birds tend to be most reclusive. In addition, the exact reproductive status of these same individuals must be known, including their ongoing participation in parental care. The latter has long been understood to be a key factor (cf. Lack 1954, Pitelka 1958) that, to our knowledge, is just now drawing close scrutiny from field biologists (Zaias and Breitwisch 1990). Finally, sample sizes must be large because of possible sex and age differences and because there are endless permutations of individual reproductive schedules related to variables such as nutritional status, habitat conditions, competition, predation, and weather.

In this paper we attempt to shed more light on this important period in the annual cycle with 8 years of molt data obtained on the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*). This is an intracontinental migrant that winters in Mexico and summers at high altitude in the western United States. Our study population occupies subalpine meadows at about 3,000 m near Tioga Pass in the Sierra Nevada of California. Females perform all of the nest building and incubating. The mating system is primarily monogamous although extra-pair fertilizations are common (Sherman and Morton 1988) and a few cases of polygyny have been observed. Pairs are usually single-brooded but readily provide replacement clutches and are, on occasion, double-brooded. A single nesting endeavor from clutch initiation to fledgling independence lasts at least 6 weeks (Morton et al. 1972a). Annual

maximum snowpack can vary by a factor of six at Tioga Pass and because snow cover strongly influences availability of nesting sites, its melting schedule can affect the phasing of *Z. l. oriantha*'s reproductive period by 4 weeks or more. In fact, 75% of the reproductive schedule, which occurs mostly in June and July, can be predicted by the maximum snowpack as measured in early April (Morton and Allan 1990). We view this variation in schedule to be an important natural event that is very helpful to our understanding of how reproduction and molt are interrelated in this migratory bird.

## METHODS

From 1980 to 1987 a regular routine of trapping *Z. l. oriantha* three or four times per week was conducted from May to October near Tioga Pass, Mono County, California. We also made daily observations of their behavior and searched for active nests. All birds captured, including nestlings, were banded with USFWS bands. Adults were also marked with unique combinations of three color bands. Breeding pairs were identified as often as possible and their last egg in a given season was used for purposes of the present study to describe the timing of reproduction with respect to molt parameters.

Data were recorded on time and location of capture, level of fat deposition, body mass, wing length, and molt status. Breeding status was monitored either by the extent of brood-patch development, length of cloacal protuberance, or gonad size; the latter being measured during laparotomies. Adults captured during postnuptial molt had all of these data taken on a routine basis. In addition, their molt status was quantified by measuring the lengths of individual primary feathers of the right wing to the nearest millimeter with a thin plastic ruler. Old primaries were those that had been present the previous year. Missing primaries were those that had been dropped but papillae of replacements were not yet visible. Missing primaries and pinfeathers were considered to be growing. Feathers that were recently and fully grown in, with hardened sheaths, were called new.

Primary molt proceeded centrifugally and simultaneously in both wings and its onset was defined by the loss of P<sub>1</sub>. Molt completion occurred when the sheath of P<sub>9</sub> (the last primary) became hardened. Estimations made regarding primary molt onset and completion date were

based on a 2-year study of *Z. l. oriantha* (Morton and Welton 1973) in which birds were held captive at the breeding area. These data on captives served as a template for this study, which was especially important in evaluating the growth of P<sub>1</sub> to determine molt onset date and of P<sub>9</sub> to determine molt completion date. The captive data also showed that the duration of primary molt encompassed 95% of the total period of postnuptial molt. Thus we feel justified in characterizing postnuptial molt dynamics, including its duration, in our wild study population from measurements of primary feathers alone.

Sometimes birds were caught more recently than the predicted onset date and were not yet molting. For example, at an individual's first capture while in molt, the length of P<sub>1</sub> might suggest that molt had begun 8 days earlier, though 7 days earlier the same individual was captured with the old P<sub>1</sub> still intact. In these cases, molt onset was assumed to be the next day, i.e., 6 days earlier. The completion of molt, likewise, often had to be estimated because birds were captured when P<sub>9</sub> was still growing and not captured again until P<sub>9</sub> was fully grown. Analogous to molt onset determinations, if the prediction of completion was later than the day of capture following molt completion then molt completion was assumed to be the day before. For example, the highest numbered growing primary gave a prediction that molt would end on 1 September. However, the bird was caught on 29 August and molt was already finished so its molt was recorded as being completed on 28 August. Duration of molt was found by subtracting onset from completion dates. It was calculated only for birds caught at least three times over a span of more than 10 days.

Birds referred to as known breeders were those in which the schedule of laying was precisely known. Parental care was assumed to end when fledglings were 26 days old because *Z. l. oriantha* young are entirely able to feed themselves at about Day 26–30 (Morton et al. 1972b). This is conservative, however, because we have sometimes observed female parents feeding young known to be more than a month old.

Since many birds were captured in multiple seasons, individuals were recognized in as many seasons as they were captured. Therefore, there was no distinction made in sample sizes inter-annually between three birds caught in one season each and one bird caught in three separate

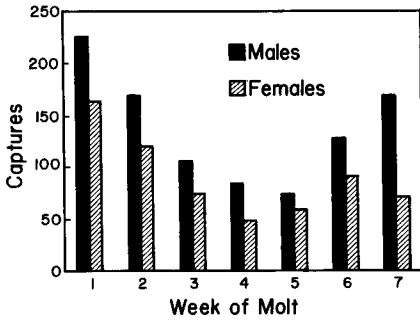


FIGURE 1. Number of captures of *Zonotrichia leucophrys oriantha* by week of postnuptial molt. Total captures: males = 962, females = 632.

seasons. We understand the statistical drawbacks involved here but molt onset and termination dates as well as molt duration all varied considerably in individuals for which we had repeated measures. This interannual variation will be the topic of a separate report.

Migration dates were defined as the date of last capture of the season following completion of molt. Since trapping was conducted on such a regular basis, it was felt that this date closely approximated the dates when individuals actually departed. Statistical analyses were made with SPSS (Nie et al. 1975) and Minitab statistical packages. Alpha levels for all tests were 0.05.

RESULTS

CAPTURE FREQUENCY DURING MOLT

In eight summers of trapping *Z. l. oriantha* at Tioga Pass, a total of 2,976 primaries were measured during 962 captures of 165 individual males. Because individuals were often captured

in multiple years (one male was caught in six different years), the total number of individual cycles of molt in males comprising all years was 230. There were 2,058 primaries measured during 632 captures of 136 females, representing 183 individual cycles of molt.

The number of captures varied in both sexes during the 7-week course of molt and, in a given week, females were never caught as often as males (Fig. 1). Capture frequency decreased through Week 5 in males and Week 4 in females, after which it tended to increase. In males this increase continued through the remainder of molt such that during Week 7 there were exactly as many captures made as in Week 2 (170). Females, however, were caught fewer times while molting in their last week than in their penultimate week. Their last week's total was still greater than the total captures made during either Week 4 or 5 and were nearly equal to those made during Week 3 (72 vs. 74).

ANNUAL MEASURES OF MOLT PARAMETERS AND TIME OF MIGRATION

Mean date of molt onset was earliest in 1987 and latest in 1980, with a range of 17 days for both sexes (Table 1). Mean date of molt completion had an interannual range of 17 days in males and 15 days in females. For all years combined, the average date of molt onset was 28 July for males and 2 August for females, whereas the average date of molt completion was 17 September in males and 19 September in females (Table 1). Plots of the molt onset data (not shown) appeared to have a normal distribution for both sexes, with the schedule for females being consistently later than the one for males. The intersexual differ-

TABLE 1. Data on molt of primary remiges in *Zonotrichia leucophrys oriantha* for each year that data were collected. Sample sizes refer to number of individual birds captured in a given year. SD units are days.

	Molt onset						Molt completion					
	Males			Females			Males			Females		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
1980	5 Aug	7.1	38	12 Aug	9.1	24	24 Sep	6.6	38	27 Sep	7.8	24
1981	26 July	4.8	26	28 July	7.9	27	14 Sep	5.7	26	13 Sep	7.6	27
1982	4 Aug	5.2	22	6 Aug	7.2	23	26 Sep	5.4	22	23 Sep	6.5	23
1983	30 July	7.6	12	4 Aug	6.8	19	20 Sep	5.9	12	21 Sep	7.0	19
1984	28 July	6.4	35	4 Aug	8.3	19	15 Sep	6.1	35	22 Sep	9.3	19
1985	25 July	7.1	30	27 July	7.3	22	14 Sep	7.1	30	14 Sep	7.4	21
1986	25 July	6.1	38	30 July	8.8	25	14 Sep	4.9	38	17 Sep	8.3	25
1987	19 July	6.0	29	26 July	5.8	24	9 Sep	4.1	29	12 Sep	6.9	23
All years	28 July	8.2	230	2 Aug	9.3	183	17 Sep	7.8	230	19 Sep	9.2	181

ences in molt onset and completion were both significantly different ( $P < 0.001$  and  $P < 0.025$ , respectively,  $t$ -tests). Mean duration of molt varied interannually by several days in both sexes (Table 1). The maximum recorded for males was 52.4 days (1982) and the minimum was 49.9 days (1981). In females the maximum duration was 51.2 days (1985) and the minimum was 47.0 days (1987). The mean molt duration for males in all years combined exceeded that of females by 2.7 days, 50.9 to 48.2 days ( $P < 0.001$ ,  $t$ -test).

The range of migration dates (see Methods) in all years combined was 42 days in males (2 September to 15 October) and 46 days (3 September to 19 October) in females. On average, males stayed 9.1 days on the study site after molt was finished before migrating, whereas females stayed 7.4 days ( $P < 0.05$ ,  $t$ -test). However, the overall average date of migration in all 8 years of the study combined was 25 September for both males and females.

#### AGE EFFECTS

There were no statistically detectable effects of age on molt onset, completion, or duration in females (Table 2). Differences were found in males, however. For example, the mean date of molt onset was earlier by 5 days in 1-year-old (yearling) males than in 2-year-olds ( $P < 0.001$ ,  $t$ -test). And 1-year-olds began molt 7 days earlier than males that were three or more years of age ( $P < 0.001$ ,  $t$ -test). The same pattern held for molt completion. Duration of molt in males did not vary significantly among the age classes ( $P > 0.05$ , all comparisons).

The average completion date of molt in 130 yearling males was 4 days before the 18 September completion date found in 110 yearling fe-

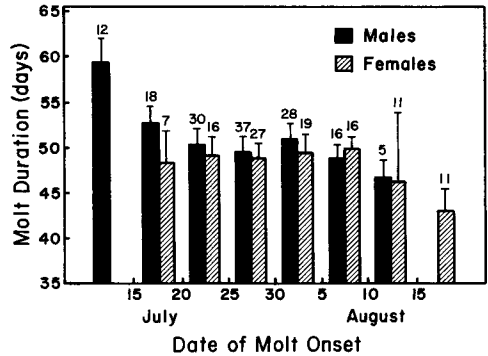


FIGURE 2. Duration of postnuptial molt in *Zonotrichia leucophrys oriantha* in relation to date of molt onset. Lines show 2SE above means and numbers above them are sample sizes.

males ( $P < 0.01$ ,  $t$ -test). However, when the 88 older males (age 2 years +) were compared to the 68 older females, there was no statistical difference in average date of molt completion (males: 19 September; females: 20 September).

#### MOLT DURATION BY DATE OF MOLT ONSET

In the first males to begin molt (15 July or earlier), mean molt duration was the longest, 59.2 days. This was significantly longer than in any of the other six class intervals of males that began molt at a later time (Fig. 2). Of these 12 earliest molting individuals, 11 were yearling males, only three of which were known to be mated. The twelfth male was 2 years old and was a known breeder. In the next group of males to begin molt (16–20 July), 14 of 18 were yearlings, and only six of these were known to be breeding. Regardless of breeding status, the total percentage of yearlings was highest in the first group of males to begin molt (92%, 11 of 12), and second highest in the second group (78%, 14 of 18). The percentages continued to decrease throughout the onset intervals to a minimum of 20% (1 of 5) of males which began molt after 10 August.

The percentage of yearling males that were known breeders was at a minimum in the earliest onset group (27%), but this percentage increased to between 42% (1–5 August) and 55% (6–10 August). Of the latest onset group of five birds, the lone yearling was a known breeder. Of the yearling males in which molt onset was determined (though duration may not have been, see Methods), 36% (46 of 129) were known breeders as compared to 61% of older males (54 of 88).

TABLE 1. Extended.

Molt duration (days)					
Males			Females		
$\bar{x}$	SD	n	$\bar{x}$	SD	n
50.1	4.1	22	47.2	4.5	17
49.9	5.2	16	47.6	6.0	14
52.4	4.9	17	48.4	4.5	18
52.0	8.6	11	47.8	5.0	9
50.2	5.3	23	49.5	5.0	12
50.6	3.5	18	51.2	3.0	10
52.3	6.1	22	47.6	3.4	12
51.7	5.7	19	47.0	3.2	15
50.9	5.3	148	48.2	4.5	107

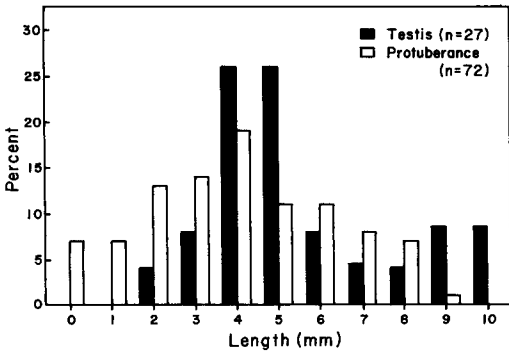


FIGURE 3. Variation in testis and cloacal protuberance length in *Zonotrichia leucophrys oriantha* on the first day of postnuptial molt (molt onset).

GONADAL CONDITION AND ONSET OF MOLT

Gonadal condition was evaluated via laparotomy in 17 females and 27 males on the day P<sub>1</sub> was found to be missing, i.e., on the first day of molt. In all females, ovaries were regressed with the largest follicles being 1 mm or less in diameter. Interestingly, they also had brood patches of various functional stages, including some that were edematous and vascularized because their bearers were incubating or brooding nestlings. In males, gonadal condition, as determined by testis length, was highly variable at onset of molt as was cloacal protuberance length (Fig. 3). Testes ranged from 2 to 10 mm in length and protuberances from 0 to 9 mm. Mean testis length on the first day of molt was  $5.7 \pm 2.4$  mm and mean protuberance length was  $4.1 \pm 2.3$  mm. Of the six males found to have started molt with testes at maximal or near-maximal lengths (9 to 10 mm), four were mated and two were not. The latter were both yearling male floaters. Two of the mated birds were yearlings and two were 2 years old.

Similar trends were found in females when yearlings and older birds were compared. However, percentages of known breeders in both female cohorts were higher than those of their male counterparts; 42% of yearling females (47 of 112), and 69% of older females (47 of 68). In both sexes, the youngest individuals tended to begin molt earlier in the season than the rest of the population and they also tended to be nonbreeders. Also, significantly fewer yearling males and females, from which we obtained molt data, were known breeders as compared to older birds ( $P < 0.01$  for both sexes,  $\chi^2$ ).

MOLT PARAMETERS IN RELATION TO REPRODUCTIVE STAGE

The later in the summer that birds were engaged in reproduction the later they began to molt. For example, when clutch completion of the last nest of the season was 15 June or earlier, mean molt onset was 24 July in males and 26 July in females (Table 3). When clutch completion was 26 July or later, molt onset occurred on average 9 days later in males (2 August) and 18 days later in females (13 August). Molt duration, on the other hand, did not appear to vary consistently with time of reproduction in either sex. Molt in those with the latest clutch completions of the season (26 July or later) had the greatest mean duration of any interval examined but within each sex this

For the 85 females that began molt before 11 August, the average molt duration was 49.1 days (Fig. 2). Duration in females whose molt began 11–15 August was 46.2 days and 42.9 days in those that began molt after 15 August. Mean duration in the 22 females beginning molt on 11 August or later was 44.6 days, a significant decrease when compared to the 85 that began molting earlier ( $P < 0.001$ , ANOVA).

TABLE 2. Parameters of primary remige molt in relation to age in *Zonotrichia leucophrys oriantha*.

Age (years)	Sex	Molt onset			Molt completion			Molt duration (days)		
		Mean date	SD (days)	n	Mean date	SD (days)	n	$\bar{x}$	SD	n
1	M	25 July	8.0	130	14 Sep	7.4	130	51.4	5.7	83
	F	1 Aug	9.4	112	18 Sep	9.5	110	48.3	4.5	63
2	M	30 July	6.8	49	18 Sep	7.3	49	49.8	4.2	35
	F	2 Aug	8.8	38	20 Sep	7.7	38	47.4	4.8	21
3–6	M	1 Aug	6.1	39	21 Sep	7.3	39	50.7	5.8	23
	F	2 Aug	7.8	30	20 Sep	8.1	30	48.4	4.1	22

TABLE 3. Mean date of molt onset and mean duration of molt by date of final clutch completion (= date when last egg was laid in the last nest of the season).

	Date of clutch completion					
	15 June or earlier	16-25 June	26 June-5 July	6-15 July	16-25 July	26 July or later
Mean date of molt onset						
Males						
$\bar{x}$	24 July	27 July	30 July	30 July	3 Aug	2 Aug
SD (days)	6.8	5.7	6.9	8.4	7.8	3.9
<i>n</i>	16	24	21	28	13	8
Females						
$\bar{x}$	26 July	31 July	31 July	5 Aug	9 Aug	13 Aug
SD (days)	7.6	6.8	6.7	7.4	11.0	8.4
<i>n</i>	17	15	20	26	8	8
Mean duration of molt (days)						
Males						
$\bar{x}$	51.1	51.4	49.1	49.5	51.1	53.8
SD	6.1	7.3	3.5	3.6	3.2	8.3
<i>n</i>	11	20	14	22	10	4
Females						
$\bar{x}$	47.1	48.3	48.3	47.7	47.5	49.3
SD	6.2	3.7	4.3	4.3	5.2	7.4
<i>n</i>	9	9	13	18	6	7

difference was not significant when compared to any of the other intervals ( $P < 0.05$ , ANOVA). Mean molt duration, in congruence with the data in Tables 1 and 2, was longer in males than in females in all cases in which they had the same reproductive schedule (Table 3).

Although the data in Table 3 indicate that the molting schedule was delayed when involvement in reproduction was prolonged, this delay was not directly proportional. That is, the slope of date of molt onset over date of clutch completion was not unity, it was in fact 0.3 days in females and 0.2 days in males. This is clearly illustrated if we examine the relationship between the date when a pair's final clutch of the season was completed and the number of days that elapsed from then until the onset of molt in those individuals (if known). As inferred above, the number of days between these events decreased steadily as date of clutch completion increased in both sexes with males always starting molt sooner on the average than females (Fig. 4). Included in these data were five cases wherein a male's molt onset followed his mate's last egg of the season by at least 50 days; all of these occurred in the earliest interval designated (last egg 15 June or earlier). At the other extreme, there were two males whose molt began even before their mate's last egg was

laid. In one case it was the day before clutch completion (16 July), and in the other, the day before the clutch was initiated (5 August). Molt onset in females ranged from a high of 65 days after laying her last egg on 19 June in one case to a low of 2 days in another bird whose last egg was laid on 5 August. The latter female was the one paired to the above-mentioned male that began molt prior to her clutch start. His molt required 64 days while hers was completed in 56 days. This pair was also known at one time to be feeding fledglings that were 15 days old.

Further analysis of the relationship between reproductive status and postnuptial molt was performed by calculating the cumulative percentage of individuals starting molt through four identifiable stages of their reproductive schedule: egg laying, incubation, nestling period, and fledging period. The cohorts compared consisted of those birds which began postnuptial molt while still with a nest (Group 1) vs. those birds which began molting at any time after their chicks had fledged (Group 2). There were 36 males and 18 females in Group 1, and 74 males and 78 females in Group 2 (Fig. 5). Only birds with precisely known reproductive histories could be used in this analysis; therefore the seasonal histories of their nests were known (Table 4). Obviously most

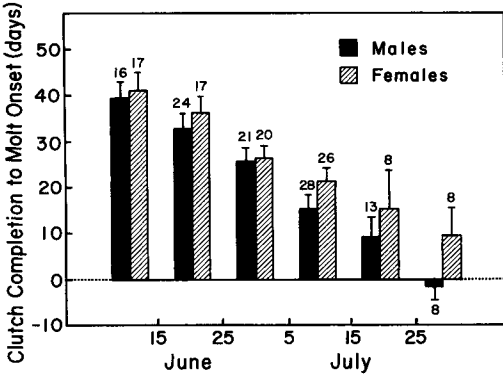


FIGURE 4. Mean number of days between completion of the season's last clutch to the date of postnuptial molt onset in *Zonotrichia leucophrys oriantha*. Lines show 2 SE above means and numbers above them are sample sizes.

of the birds that had only one nest belonged to Group 2 whereas most of those that were able to bring off two broods belonged to Group 1.

In both sexes onset of molt overlapped substantially with reproductive events, more so in males than in females since males tended to begin molt earlier than females throughout the reproductive cycle. Two males of 110 (2%) began molt before their mates had finished laying, and 15 (14%) of them as well as 8 of 96 females (8%) began molt before incubation was completed. Nineteen males (17%) and 10 females (10%) began molt during the nestling period. Thus a total of 36 males (33%) and 18 females (19%) had initiated postnuptial molt before their chicks had fledged. Also, 84 males (76%) and 68 females (71%) began molting before their fledglings were independent (Fig. 5).

The rate of molt onset (the percentage of individuals of each sex starting molt per day during the various stages of reproduction), was greater in males than in females for birds which began molt during egg laying (0.4 to 0.0% per day), incubation (1.0 to 0.8% per day), and during the nestling period (1.9 to 1.0% per day). When fledglings were present the rate of molt onset in males increased to 2.7% per day (48 of 110 birds in 16 days), but the rate increased even more in females to 3.2% per day (50 of 96 birds in 16 days). The fledgling period corresponded to the time when chicks were out of the nest but had not yet achieved independence from parental care (from about 21 days to 37 days after their parents' last

TABLE 4. Seasonal histories of *Zonotrichia leucophrys oriantha* nests used for data shown in Figure 5. Groups 1 and 2 are defined in text.

Nest histories within the season	Males		Females	
	Group 1	Group 2	Group 1	Group 2
First (and only) nests	8	57	4	56
Replacement nests	16	15	8	20
Second nests*	12	2	6	2
Total number of nests	36	74	18	78

\* Double broods, i.e., fledglings had already been produced from an earlier nest that season.

egg). After fledglings had become independent, males once again entered molt more rapidly than females (1.4% to 1.0% per day). Onset of molt following the completion of parental care occurred in 24% of all males (26 of 110) and 29% of all females (28 of 96).

COMPARISONS OF GROUP 1 AND GROUP 2 BIRDS

*Molt parameters.* The average number of days that elapsed following loss of P<sub>1</sub> before all other individual primaries were shed was always greater in Group 1 than in Group 2 birds of both sexes (Table 5) and the difference was significant in both sexes (Table 6). In males, the overall delays in shedding of primaries in Group 1 compared to Group 2 averaged 1.8 days. The greatest delay occurred for P<sub>3</sub>, 3.2 days, although P<sub>4</sub> and P<sub>9</sub> were also delayed by more than 2 days (2.3 and 2.5 days, respectively). In females, the overall delays in shedding averaged 4.1 days with P<sub>3</sub> being 3.9 and P<sub>6</sub> through P<sub>9</sub> all being delayed by more than 4 days (4.3, 5.8, 5.0, and 6.1, respectively). Except for P<sub>2</sub> in Group 1 birds, primaries of females (P<sub>3</sub>-P<sub>9</sub>) dropped later than those of males. In Group 2 individuals, P<sub>2</sub>-P<sub>4</sub> dropped earlier in males while the other primaries (P<sub>5</sub>-P<sub>9</sub>) were shed later in females.

In any individual of Group 1, the maximum length that P<sub>2</sub> attained before P<sub>3</sub> was shed was 38 mm in a male and 34 mm in a female. The day of molt in these two extreme examples was the 15th and 14th days, respectively. The same male was captured on his 17th day of molt and P<sub>2</sub> was 41 mm and P<sub>3</sub> was only 1 mm. There were two Group 2 males which grew P<sub>2</sub> to 25 mm with P<sub>3</sub> still intact. One male was captured on his ninth day of molt and the other on his 10th day. The most extreme case noted among Group 2 females was one where P<sub>2</sub> had reached



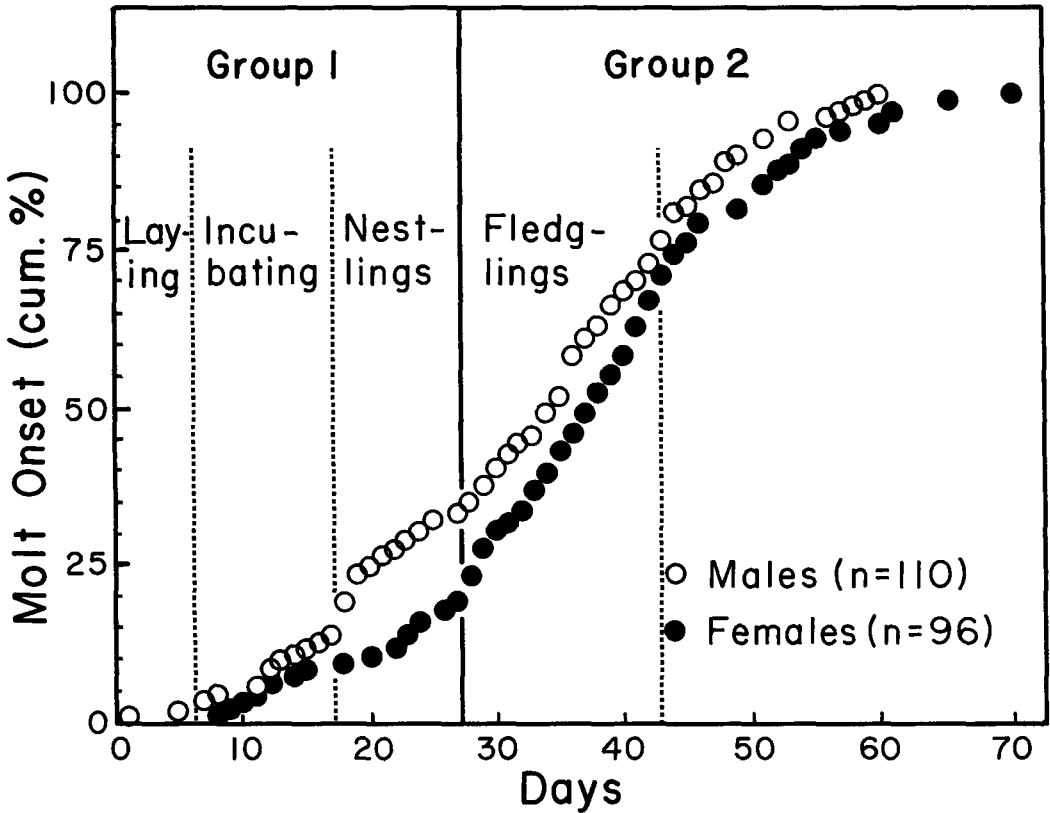


FIGURE 5. Cumulative percentage of *Zonotrichia leucophrys oriantha* entering postnuptial molt relative to their stage of reproduction. Group 1 birds began molting prior to when their chicks fledged, Group 2 birds afterward.

23 mm on the eighth day of her molt and the old P<sub>3</sub> was still intact.

In terms of millimeters of growth per day in individual primaries, P<sub>1</sub> and P<sub>2</sub> showed a slower though comparable growth in Group 1 vs. Group 2 birds whereas all other primaries exhibited an accelerated growth, with the differences being most noticeable in P<sub>3</sub> of females (Table 5). Although Group 1 females dropped P<sub>3</sub> nearly 4 days later than those in Group 2, the former completed 80% of P<sub>3</sub> growth barely 1 day later than the latter. Pairwise comparisons of growth rates for P<sub>3</sub>–P<sub>9</sub> indicate that this group of seven feathers grew significantly faster in Group 1 than in Group 2 females (Tables 5, 6).

Table 5 also relates the day of molt at which primaries attained 80% of their total length. Both sexes reached this limit of linear growth (which we have defined for our purposes as being 80% of full length) in P<sub>1</sub> and P<sub>2</sub> later in molt in Group

1 than in Group 2 birds. Beyond that point in the wing, Group 1 and 2 males had similar schedules which were not different statistically (Table 6). Since growth rates of primaries was slowed in Group 1 females (see above) their attainment of 80% lengths should also have been significantly slower, and it was (Table 6).

There was not a significant difference throughout molt in the average number of primaries growing simultaneously in Group 1 vs. Group 2 males although there was in females. Males averaged 2.9 primaries in simultaneous growth in Group 1 and 3.1 in Group 2 birds ( $P > 0.1$ , Mann-Whitney *U*). Females in Group 1 averaged 3.0 whereas those in Group 2 averaged 3.3 primaries in simultaneous growth ( $P < 0.05$ , Mann-Whitney *U*). During Week 2 Group 1 females averaged only 2.8 primaries growing whereas those in Group 2 averaged 4.4. This difference was highly significant ( $P < 0.001$ , *t*-test). Their

TABLE 5. Data on dynamics of postnuptial molt in Group 1 and Group 2 *Zonotrichia leucophrys oriantha*.

Primary number	Group 1					Group 2				
	Day shed	Shedding interval (days)	Growth rate (mm/day)	Day when 80%	n	Day shed	Shedding interval (days)	Growth rate (mm/day)	Day when 80%	n
<b>Males</b>										
1	0.0	—	2.7	16.7	36	0.0	—	3.4	13.4	159
2	2.2	2.2	2.9	18.3	26	0.6	0.6	3.1	15.6	148
3	5.0	2.8	3.2	19.8	24	1.8	1.2	2.5	20.9	134
4	7.5	2.5	3.2	22.8	22	5.2	3.4	2.8	22.4	86
5	10.6	3.1	2.8	28.6	19	10.1	4.9	3.2	25.9	75
6	15.4	4.8	2.7	34.9	20	13.8	3.7	2.6	34.6	62
7	19.3	3.9	2.5	40.0	19	18.0	4.2	2.2	41.3	56
8	21.4	2.1	2.3	43.5	21	19.6	1.6	2.2	43.3	57
9	23.5	2.1	1.9	47.7	24	21.0	1.4	1.2	49.9	89
<b>Females</b>										
1	0.0	—	2.7	16.4	18	0.0	—	3.6	15.0	140
2	2.1	2.1	3.1	16.9	17	0.6	0.6	3.3	15.0	136
3	6.2	4.1	4.0	17.9	17	2.3	1.7	3.0	16.7	112
4	8.6	2.4	3.2	23.4	12	5.3	3.0	3.0	22.2	81
5	10.8	2.2	2.6	29.5	9	7.7	2.4	2.3	28.9	57
6	15.9	5.1	2.6	35.0	8	11.6	3.9	2.5	32.3	42
7	20.6	4.7	2.8	37.8	11	14.8	3.2	2.4	37.5	41
8	22.5	1.9	2.5	41.6	14	17.5	2.7	2.3	41.1	50
9	24.3	1.8	2.2	45.0	14	18.2	0.7	1.9	42.6	58

patterns during the remainder of molt were quite similar, however (Fig. 6).

How did molt onset and completion dates vary in Group 1 vs. Group 2 birds and did the differences in shedding times of primaries and their growth rates affect molt duration? The answers are that the two groups had schedules that were not different by calendar date (Table 7). Molt duration was also apparently unaffected by time of onset with regard to reproductive schedule in males but it was in females. In the latter, molt duration was significantly longer in Group 1 than in Group 2 members (Table 7).

During our examinations of individual histories we came to realize that molt was greatly slowed or inhibited in its earliest stages in some

of the birds that began molting before their chicks had fledged, i.e., in some Group 1 birds. The scope of this inhibition was simply not apparent, however, when data from all Group 1 birds were lumped together as we have done thus far. To rectify this and to illustrate the condition of molt inhibition more clearly, we have selected data from four individuals (one male and one female from each group), all of which were in their 17th day of postnuptial molt. At that point in their schedule the Group 2 birds had already finished growing P<sub>1</sub> and P<sub>2</sub> and had commenced growth in the next four primaries (Fig. 7). In contrast, P<sub>1</sub> and P<sub>2</sub> were not yet fully grown in the Group 1 birds, P<sub>3</sub> had just been shed, and the remaining primaries were still old. These data are not rep-

TABLE 6. Probability values obtained in comparison of primary remige molt data obtained from Table 5 (Wilcoxon's matched-pairs ranked-signs test, two-tailed *P*).

	Group 1 vs. Group 2	
	Males	Females
Day of molt that primary was shed (P <sub>2</sub> -P <sub>9</sub> )	0.012	0.012
Shedding interval between primaries (P <sub>2</sub> -P <sub>9</sub> )	0.484	0.093
Growth rate (P <sub>1</sub> -P <sub>9</sub> )	0.441	0.155
(P <sub>3</sub> -P <sub>9</sub> )	0.108	0.018
Day when 80% of total length was reached (P <sub>1</sub> -P <sub>9</sub> )	0.374	0.008

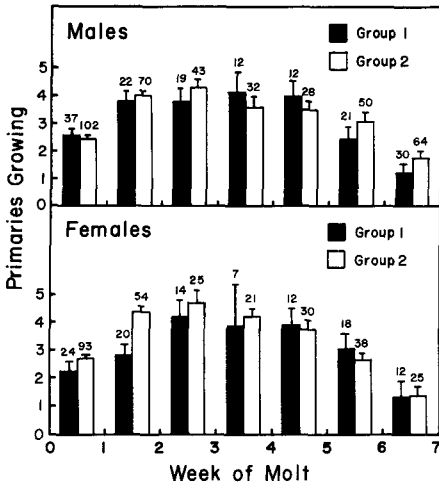


FIGURE 6. Number of primaries growing simultaneously during the course of postnuptial molt in Group 1 and Group 2 *Zonotrichia leucophrys oriantha* males and females. Lines show 2 SE above means and numbers above them are sample sizes.

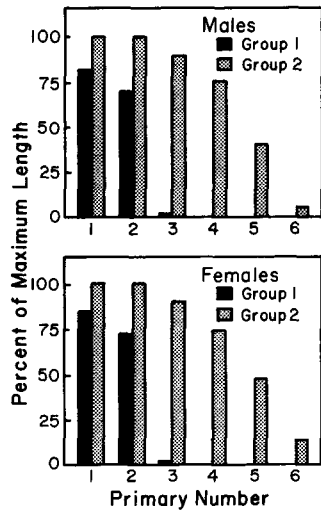


FIGURE 7. Percentage of maximum length attained in Primaries 1-6 on 17th day of postnuptial molt in two male (one of Group 1 and one of Group 2, upper panel) and in two female (one of Group 1 and one of Group 2, lower panel) *Zonotrichia leucophrys oriantha*.

representative of all members of these groups, they have been deliberately selected to show the marked contrasting conditions in molt that we knew to exist among individuals depending upon when they began molt with respect to their reproductive cycle, and they serve to illustrate that inhibition occurred because there was both an increase in the shedding intervals of P2 and P3 and a decrease in growth rates of P1 and P2.

The mean number of individual primaries growing simultaneously showed similar trends in both sexes in that it increased from two or three feathers during the first week of molt to four or five feathers during the third week and then declined thereafter (see Fig. 6 for pattern). In males,

the mean number of primaries growing simultaneously throughout molt was statistically independent of molt onset ( $P > 0.05$ , ANOVA). This was not true of females. Those beginning molt earliest and latest in the season grew the greatest mean number of primaries simultaneously during molt:  $3.5 \pm 1.6$ , onset 21 July or earlier and  $3.6 \pm 1.4$ , onset 16 August or later. At other onset times the numbers were lower than in these two groups, although only in females that began molt between 6-10 August was the difference significant ( $\bar{x} = 3.0 \pm 1.5$ ;  $P < 0.025$ ). Individual males were never found to be growing more than six primaries simultaneously, although twice females were captured with seven

TABLE 7. Parameters of postnuptial molt in Group 1 and Group 2 *Zonotrichia leucophrys oriantha*.

	Group 1			Group 2			P
	Mean	SD (days)	n	Mean	SD (days)	n	
<b>Males</b>							
Molt onset date	28 July	6.9	36	31 July	7.6	74	ns
Molt completion date	17 Sep	8.0	36	19 Sep	7.6	74	ns
Molt duration (days)	51.1	4.6	25	50.4	5.8	51	ns
<b>Females</b>							
Molt onset date	1 Aug	8.6	18	4 Aug	9.6	77	ns
Molt completion date	20 Sep	9.2	18	20 Sep	9.3	78	ns
Molt duration (days)	49.9	4.9	18	47.1	4.8	47	<0.05

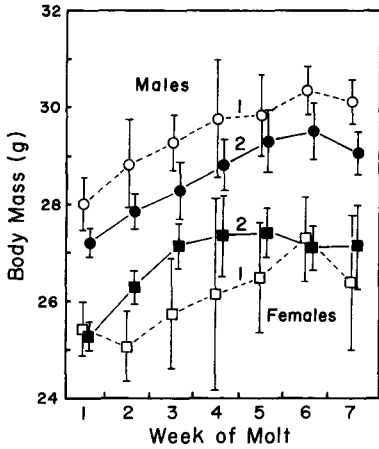


FIGURE 8. Mean body mass during postnuptial molt in Group 1 (open symbols) and Group 2 (filled symbols) *Zonotrichia leucophrys oriantha*. Sample sizes for means ranged from 9 to 50 in females (squares) and from 16 to 75 in males (circles). Bars show 2 SE above and below the means.

primaries growing simultaneously. The grand mean number of primaries growing simultaneously in females throughout molt,  $3.3 \pm 1.4$ , was greater than the mean number growing in males,  $3.1 \pm 1.4$  ( $P < 0.025$ , *t*-test).

**Body mass.** For the population as a whole, body mass increased steadily by a total amount of about 2 g from Week 1 through Week 6 of molt (males 2.2 g; females 1.9 g), with the greatest rates of gain occurring in the first 3 weeks of molt. Both males and females tended to lose mass during Week 7, although in neither case were their average masses significantly different than in the previous week. In each week of molt the mean mass of males was always at least 2 g more than that of females, with a maximum difference of 2.6 g occurring during Weeks 5 and 6. The total mean mass of males during molt was 2.4 g greater

than that of females (28.7 g vs. 26.3 g,  $P < 0.001$ , *t*-test).

When body mass data were examined by sex for the subset of birds in Groups 1 and 2, we observed that males tended to increase steadily in mass during molt (Fig. 8) with Group 1 birds being consistently about 1 g heavier than their counterparts in Group 2 ( $P < 0.001$ , ANOVA). In females, the story was quite different. Group 1 birds generally weighed less than those in Group 2 at a comparable week of molt although the difference was significant only in Weeks 2 and 3 ( $P < 0.05$ ). Body masses of females, when considered for the full duration of molt, were not different for the two groups.

Molt tended to begin and end slightly earlier in both males and females of Group 1 than in those in Group 2 although the differences were not significant. Molt duration was slightly longer in the Group 1 birds, however, significantly so in females (Table 7).

**Reproductive success.** The percentage of successful nests (those fledging at least one young) was higher for Group 2 than Group 1 birds although the difference was significant only for males (sample sizes were considerably smaller for females; in only 18 cases were we able to obtain good molt data on those that had started molting with nestlings or earlier; Table 8). Actual numbers of fledglings produced per nest were significantly greater for Group 2 birds of both sexes (Table 8).

DISCUSSION

CAPTURE FREQUENCIES

Our capture frequency data indicate that the behavior of adult *Z. l. oriantha* changed as they proceeded through postnuptial molt (Fig. 1). Although males appeared to be easier to trap than females at all times, thus nearly always affecting the comparative sample sizes, both sexes were

TABLE 8. Reproductive success in Group 1 and Group 2 *Zonotrichia leucophrys oriantha*. Percentage of successful nests, significance tested with  $\chi^2$ , and chicks fledged per nest with *t*-test.

	Males		P	Females		P
	Group 1	Group 2		Group 1	Group 2	
Number of nests	34	71	—	18	77	—
% successful <sup>a</sup>	52.9	74.9	<0.05	61.1	79.2	ns
Chicks fledged/nest						
$\bar{x}$ (SD)	1.29 (1.34)	2.49 (1.66)	<0.01	1.72 (1.60)	2.54 (1.61)	<0.05

<sup>a</sup> Fledged at least one chick.

more reluctant to enter traps at midmolt than at the beginning or end of molt. Also, heavily molting males did not sing and although both sexes remained on their usual territories, they were difficult to flush and observe. Similar skulking behavior was noticed in molting Eurasian Bullfinches *Pyrrhula pyrrhula* (Newton 1966).

#### ANNUAL VARIATION IN MOLT ONSET, COMPLETION AND DURATION

The degree of variation in the timing and rate of postnuptial molt from year to year in a free-living population provides useful information on how this process is controlled or affected by both ecological and evolutionary factors. We found that molt consistently occurred earlier and was of a longer duration in males than in females. Mean onset date varied interannually by 17 days in both sexes and mean completion date by 17 days in males and 15 days in females whereas mean duration varied by 2.5 days in males and 4.0 days in females (Table 1). In contrast, the reproductive schedule, as represented by mean date of clutch initiations, varied by 25 days (12 June 1987 to 7 July 1980, 1983) during this same 8-year period (M. L. Morton, unpubl. data). Total interannual variation in reproductive schedule is known to be a month or more in the Tioga Pass population, however (Morton 1978, Morton and Allan 1990).

Molt duration showed little interannual variation (Table 1), but it was the one parameter measured that differed with age, and then in males only (Table 2). This was due to the fact that molt was more protracted in unmated, floater males, the greatest share of which were yearlings (see also Morton et al. 1990). These yearling floaters were also among the first individuals to enter molt each season. A similar response occurs in Stellar's Jays *Cyanocitta stelleri* (Pitelka 1958) and in Cassin's Finches *Carpodacus cassinii* (Samson 1976). Molt duration also had another seasonal component in that it tended to decrease in the very latest birds to begin molt, especially in females.

#### MOLT AND REPRODUCTION

Interactions among molt and reproductive condition were found to be complex and highly variable. For example, on the very first day of molt, testicular and cloacal protuberance lengths (Fig. 3) varied over nearly the full range measured on the summering grounds (Morton and Allan 1990,

Morton et al. 1990). Plasma testosterone levels, however, were consistently at their seasonal low in molting males (Morton et al. 1990). These results suggest that testicular size is not a reliable indicator of secretory activity. Furthermore, there is clearly not a fixed-phase relationship between the onset of postnuptial molt and testicular regression—a conclusion reached earlier by Farner et al. (1980) from data on captive *Z. l. gambelii*. Nor is there a fixed relationship between the termination of reproductive effort (as indexed by completion of a season's final clutch) and molt onset in *Z. l. oriantha*. Molt onset occurred later if reproduction ended later (Table 3) but the interval between these events decreased by a total of 6 or 7 weeks between early June and late July (Fig. 4). The major consequence of this would appear inevitably to be a substantial overlapping of reproductive and molting schedules.

A detailed analysis of the relationship between completion of the season's final clutch and the time interval thereafter before molt onset occurred showed that about 40 days elapsed between these events in those birds that ceased reproduction in early June (Fig. 4). This interval decreased steadily thereafter, more so in males than in females, as clutch completion date became later. These data indicate that molt began in many *Z. l. oriantha* while they were still engaged in reproductive activities. A plot of molt onset in known individuals in relation to stages of their reproductive cycle shows clearly that molt was initiated in more than 70% of them before parental duties had been completed (Fig. 5). A few individuals of both sexes even began to molt before their eggs had hatched.

In order to evaluate the possible effects of these overlapping schedules, we defined two cohorts for purposes of comparison, those that began molt with nestlings or earlier, Group 1, and those that began molt with fledglings or later, Group 2 (see Fig. 5). Effects on molt dynamics imposed by concurrence of reproductive activities with molt should, of course, be more noticeable in Group 1 than in Group 2 birds. In gross aspect, however, molt was mostly unaffected. Mean onset and completion dates were not different for either sex in the two groups. Molt duration was also unaffected in males but it was significantly longer, by almost 3 days, in Group 1 than in Group 2 females (Table 7). Some differences between the two groups were also found among the fine details of their molt dynamics. For example, P<sub>2</sub>

and P<sub>3</sub> were usually shed soon after P<sub>1</sub> in Group 2 birds. By comparison, this process was considerably delayed in Group 1 birds (Table 5). Shedding intervals between individual primaries in Group 2 birds tended to increase through P<sub>5</sub>, remain high through P<sub>7</sub>, then decrease sharply in P<sub>8</sub> and P<sub>9</sub> (Table 5). A similar pattern occurred in Group 1 birds except that the shedding intervals through P<sub>3</sub> were increased. Although this occurred in both sexes, the number of primaries found to be growing simultaneously in the first weeks of molt was affected only in females (Fig. 6). Nonetheless, some individuals of both sexes were strongly affected and identified (Fig. 7). Not all members of Group 1 had such a distorted molt as those illustrated in Figure 7, but our ability to present highly accurate comparisons is limited because of the lack of a complete data set on every individual.

Despite the early differences in shedding intervals noted in Groups 1 and 2, total duration of molt was different only in females (Table 7). Compensation could occur by decreasing the shedding intervals between primaries thereby growing more of these simultaneously, a pattern that was noted in free-living *Z. l. gambelii* (Wingfield and Farner 1979), and/or by increased growth rates of the individual feathers. Our data do not show evidence for the former (see Fig. 6), but the latter did occur. Growth rates of P<sub>1</sub> and P<sub>2</sub> were lower in Group 1 than in Group 2 birds but as the remaining primaries (P<sub>3</sub>–P<sub>9</sub>) came in their growth rates were invariably higher in Group 1 than in Group 2 birds, with the lone exception of P<sub>5</sub> in males (Table 5). The increased growth rates observed in P<sub>3</sub>–P<sub>9</sub> in Group 1 birds was significant only in females, however (Table 6). Interestingly, previous studies on captive *Z. l. gambelii* indicate that growth rates of primaries were invariant in adequately nourished individuals. Altered molt durations are expected, therefore, to be due to changes in shedding intervals (Chilgren 1978, Murphy and King 1984). Only when birds were demonstrably malnourished was molt duration lengthened by both increased shedding intervals and decreased feather growth rates (Murphy et al. 1988). Highly pertinent to our results is that the expected dates of molt onset were usually unaffected in the experiments performed by these investigators.

An important variable impacting our study was a sexual difference in involvement in parental care. We know of at least four patterns. They are: (1) Parental duties are shared equally once hatch-

ing has occurred. Both parents feed the nestlings then split the brood at fledging time (Morton et al. 1972b; M. L. Morton, unpubl.). (2) As above, except that the female may initiate a second brood within a few days after fledging of the first brood. In these cases, the male appears to continue with the care of all the fledglings alone. (3) Both parents feed the nestlings but the male then provides little or no care to fledglings (see example in Morton et al. 1972b). (4) All parental care is provided by the female. We have seen this several times in situations where replacement clutches were laid late in the season. The males in these cases, when we could find them, were invariably in heavy molt. We do not have good quantitative information on the relative frequencies of these four patterns but are fairly certain that number 1 is by far the most common with patterns 2 and 3 or variations upon them being next in frequency and pattern 4 being the least common. We think that patterns 3 and 4 are often present in Group 1 birds and that pattern 1 prevails in Group 2 birds.

Apparently these differences in parental care can affect body mass during molt when the two functions are concurrent. Body mass is well-known to increase during postnuptial molt in captive *Z. l. gambelii* (King et al. 1965, Morton et al. 1969) and in both captive and free-living *Z. l. oriantha* (Morton and Welton 1973). This is probably due to an increase in blood volume (Chilgren and DeGraw 1977, DeGraw and Kern 1985) and perhaps to some deposition of fat (Morton and Welton 1973, Morton et al. 1973). We saw the usual increase in body mass in our study but its magnitude was quite different in the two groups. Group 1 males were heavier than their Group 2 counterparts whereas the reverse was true of females (Fig. 8). We attribute this to differences in energy expenditure associated with parental care. When males began molting early in the nesting cycle (Group 1), they apparently reduced greatly or eliminated altogether their efforts to feed the young. This shifted the burden of parental care to the females and the increased energy demands upon them can be discerned in their lower body masses. We know from a previous study (Mead and Morton 1985) that if the female is forced to feed nestlings by herself (male was trapped and held captive), the nestlings show reduced rates of growth and brood reduction may occur. A comparison of reproductive success in the two groups of birds identified in the present study (Table 8) is consistent with those data in

that Group 2 birds, wherein molt began late in the nesting cycle and parental care was probably provided in most cases by both sexes, fledged more young than Group 1 birds wherein molt began early in the nesting cycle and parental care was provided mostly or exclusively by the females.

Our synthesis of this body of data leads us to conclude that the postnuptial molt schedule in *Z. l. oriantha* is controlled largely independently from that of reproduction. Evidence for this is that induction of molt was found to occur at all phases of the nesting cycle. This led at times to considerable temporal overlap of the two functions in our study population because about 75% of the individuals engaged in reproduction began molting before parental care had ceased (Fig. 5). Furthermore, and this would seem to be of major significance, although the mean calendar date when molt began varied interannually by more than 2 weeks (Table 1), this date was not different in Group 1 and Group 2 birds (Table 7). It would seem to follow that there is a definite, separately fixed molting schedule. Corollaries are that gonadal condition should be highly variable at the time of molt onset, and that the separation in reproductive and molting schedules should diminish, leading to increased overlap, as the summer progresses. Both of the latter predictions are borne out by the data shown in Figures 3 and 4.

Why does postnuptial molt proceed even when reproductive efforts are still underway? To us the logical explanation is that there has been strong selective pressure for migration to occur in high altitude populations within a fairly narrow time frame or at least before trophic conditions deteriorate substantially. Insect populations decline greatly in September at Tioga Pass (Morton and Morton 1987) and snowstorms then or in October often cause other primary foods of *Z. l. oriantha*, such as grass seeds, to become covered and relatively unavailable for several days or more at a time. The acquisition of fresh plumage and of adequate fat reserves would seem to be prerequisites for successful migration. Both require substantial investments of time and energy and if migration is to occur at the most propitious time, so must it be preceded by the timely scheduling of these events, especially molt. With a full array of flight feathers in good condition *Z. l. oriantha* could at least escape to lower elevations and fatten there if necessary.

That reproduction still persists into the molting period despite reduced success along with

altered roles in parental care by the sexes is additional intriguing information on mechanisms terminating reproduction and possibly initiating molt and on parental investment. It also clearly underscores two of the many principles outlined in a recent essay by King and Murphy (1985) on the nutritional ecology of endotherms. One is that self-maintenance functions such as molt appear to be highly resistant to nutritional deficiencies, perhaps even more so than reproduction. Another is that although processes of the annual cycle such as reproduction and molt are energetically costly, it should not be assumed a priori that these requirements are decisive proximate regulators of events within the annual cycle. As King and Murphy so presciently state, the limits of tolerance of an organism to nutritional or energetic demands can only be properly evaluated within the context of its own life-history pattern.

#### LITERATURE CITED

- BANCROFT, G. T., AND G. E. WOOLFENDEN. 1982. The molt of Scrub Jays and Blue Jays in Florida. Ornithol. Monogr. No. 29. American Ornithologists' Union, Washington, DC.
- CHILGREN, J. D. 1978. Effect of photoperiod and temperature on postnuptial molt in captive White-crowned Sparrows. Condor 80:222-229.
- CHILGREN, J. D., AND W. A. DEGRAW. 1977. Some blood characteristics of White-crowned Sparrows during molt. Auk 94:169-171.
- DEGRAW, W. A., AND M. D. KERN. 1985. Changes in the blood and plasma volume of Harris' Sparrows during postnuptial molt. Comp. Biochem. Physiol. A. Comp. Physiol. 81:889-893.
- FARNER, D. S. 1983. Some recent advances in avian physiology. J. Yamashina Inst. Ornithol. 15:97-140.
- FARNER, D. S., R. S. DONHAM, M. C. MOORE, AND R. A. LEWIS. 1980. The temporal relationship between the cycle of testicular development and molt in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. Auk 97:63-75.
- FOSTER, M. S. 1975. The overlap of molting and breeding in some tropical birds. Condor 77:304-314.
- JEHL, J. R. 1968. The breeding biology of Smith's Longspur. Wilson Bull. 80:123-149.
- KENDEIGH, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. Auk 66:113-127.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. Publ. Nuttall Ornithol. Club 15:48-85.
- KING, J. R., D. S. FARNER, AND M. L. MORTON. 1965. The lipid reserves of White-crowned Sparrows on the breeding ground in central Alaska. Auk 82:236-252.
- KING, J. R., AND M. E. MURPHY. 1985. Periods of

- nutritional stress in the annual cycles of endotherms: fact or fiction? *Am. Zool.* 25:955-964.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Oxford.
- MEAD, P., AND M. L. MORTON. 1985. Hatching asynchrony in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait? *Auk* 102:781-792.
- MEWALDT, L. R., AND J. R. KING. 1978. Latitudinal variation of postnuptial molt in Pacific Coast White-crowned Sparrows. *Auk* 95:168-179.
- MILLER, A. H. 1961. Molt cycles in equatorial Andean Sparrows. *Condor* 63:143-161.
- MOORE, M. C., R. S. DONHAM, AND D. S. FARNER. 1982. Physiological preparation for autumnal migration in White-crowned Sparrows. *Condor* 84:410-419.
- MORTON, M. L. 1978. Snow conditions and the onset of breeding in the Mountain White-crowned Sparrow. *Condor* 80:285-289.
- MORTON, M. L., AND N. ALLAN. 1990. Effects of snowpack and age on reproductive schedules and testosterone levels in male White-crowned Sparrows in a montane environment, p. 235-249. *In* M. Wada, S. Ishi, and C. G. Scanes [eds.], *Endocrinology of birds: molecular to behavioral*. Japan Scientific Societies Press, Tokyo/Springer-Verlag, Berlin.
- MORTON, M. L., J. L. HORSTMANN, AND C. CAREY. 1973. Body weights and lipids of summering Mountain White-crowned Sparrows in California. *Auk* 90:83-93.
- MORTON, M. L., J. L. HORSTMANN, AND J. M. OSBORN. 1972a. 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 postjuvinal molt in White-crowned Sparrows in central Alaska. *Condor* 71:376-385.
- MORTON, M. L., AND G. A. MORTON. 1987. Seasonal changes in bill length in summering Mountain White-crowned Sparrows. *Condor* 89:197-200.
- MORTON, M. L., J. E. OREJUELA, AND S. M. BUDD. 1972b. The biology of immature Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on the breeding ground. *Condor* 74:423-430.
- MORTON, M. L., L. E. PETERSON, D. M. BURNS, AND N. ALLAN. 1990. Seasonal and age-related changes in plasma testosterone levels in Mountain White-crowned Sparrows. *Condor* 92:166-173.
- MORTON, M. L., AND D. E. 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.
- MURPHY, M. E., AND J. R. KING. 1984. Dietary sulfur amino acid availability and molt dynamics in White-crowned Sparrows. *Auk* 101:164-167.
- MURPHY, M. E., J. R. KING, AND J. LU. 1988. Malnutrition during the postnuptial molt of White-crowned Sparrows: feather growth and quality. *Can. J. Zool.* 66:1403-1413.
- NEWTON, I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108:41-67.
- NIE, R. H., C. H. HALL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. 2nd ed. McGraw-Hill, New York.
- ORELL, M., AND M. OJANEN. 1980. Overlap between breeding and moulting in the Great Tit *Parus major* and Willow Tit *P. montanus* in northern Finland. *Ornis Scand.* 11:43-49.
- PAYNE, R. B. 1969. Overlap of breeding and molting schedules in a collection of African birds. *Condor* 71:140-145.
- PAYNE, R. B. 1972. Mechanisms and control of molt, p. 103-155. *In* D. S. Farnar and J. R. King [eds.], *Avian biology*. Vol. 2. Academic Press, New York.
- PITELKA, F. A. 1958. Timing of molt in Stellar Jays of the Queen Charlotte Islands, British Columbia. *Condor* 60:38-49.
- RUNFELDT, S., AND J. C. WINGFIELD. 1985. Experimentally prolonged sexual activity in female sparrows delays termination of reproductive activity in their untreated mates. *Anim. Behav.* 33:403-410.
- SAMSON, F. B. 1976. Pterylosis and molt in Cassin's Finch. *Condor* 78:505-511.
- SCHLEUSSNER, G., J. P. DITTAMI, AND E. GWINNER. 1985. Testosterone implants affect molt in male European Starlings, *Sturnus vulgaris*. *Physiol. Zool.* 58:597-604.
- SELANDER, R. K. 1958. Age determination and molt in the Boat-tailed Grackle. *Condor* 60:355-376.
- SHERMAN, P., AND M. L. MORTON. 1988. Extra-pair fertilizations in Mountain White-crowned Sparrows. *Behav. Ecol. Sociobiol.* 22:413-420.
- STRESEMANN, E., AND V. STRESEMANN. 1966. Die Mauser der Vögel. *J. Ornithol.* 107:1-447.
- THOMPSON, J. J. 1988. The post-nuptial moult of *Quelea quelea* in relation to breeding in Kenya. *J. Trop. Ecol.* 4:373-380.
- VERBEEK, N. A. 1970. Breeding ecology of the Water Pipit. *Auk* 87:425-451.
- WINGFIELD, J. C., AND D. S. FARNER. 1977. Zur Endokrinologie des Fortpflanzungszyklus von *Zonotrichia leucophrys pugetensis*. *Die Vögelwarte* 29:25-32.
- WINGFIELD, J. C., AND D. S. FARNER. 1978a. The endocrinology of a natural breeding population of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). *Physiol. Zool.* 51:188-205.
- WINGFIELD, J. C., AND D. S. FARNER. 1978b. The annual cycle of plasma irLH and steroid hormones in feral populations of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. *Biol. Reprod.* 19:1046-1056.
- WINGFIELD, J. C., AND D. S. FARNER. 1979. Some endocrine correlates of reneating after loss of clutch or brood in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. *Gen. Comp. Endocrinol.* 38:322-331.
- ZAIAS, J., AND R. BREITWISCH. 1990. Molt-breeding overlap in Northern Mockingbirds. *Auk* 107:414-416.