

BODY WEIGHTS AND LIPIDS OF SUMMERING MOUNTAIN WHITE-CROWNED SPARROWS IN CALIFORNIA

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THE ability of migratory birds to accumulate energy in the form of fat before and during their semiannual movements between breeding and wintering grounds is one of the most striking metabolic adjustments made by any animal group. In many North American finches it is clear that the extra calories accumulated during vernal premigratory fattening are the direct result of hyperphagia induced by lengthened photoperiods. The hyperphagic response appears to be timed precisely and it causes fat deposits that constitute about 15 percent of total body weight in intracontinental migrant finches (see reviews by King and Farner, 1965; King, 1970).

Although the total energetic demands of autumnal migration must be approximately equivalent to those of vernal migration, for many species autumnal premigratory fattening appears to be more protracted and is less precisely timed than spring premigratory fattening (King, 1963; King et al., 1963; Johnston, 1964). The autumnal response has not been investigated extensively, and conclusions regarding it are still only tentative.

Much of the theory concerning premigratory fattening has been derived from data on crowned sparrows (*Zonotrichia* spp.). This group has been studied intensively with regard to the bioenergetics of migration, but thus far only one of those studies has dealt with autumnal premigratory fattening (King et al., 1965).

Herein we report on body weight and lipid changes in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) while they are on their breeding grounds in the central Sierra Nevada. Members of this race breed in high mountain meadows in the western United States and southwestern Canada, and migrate between these areas and their winter quarters in Mexico and the southwestern United States (A.O.U., 1957). We report also our observations of *Z. l. gambelii* that stopped over at the study area during their autumn migration. Members of this race are also confined to western North America. Their breeding range extends from about the southwestern border of Canada to near the arctic circle in Alaska, and they winter in lowland areas from southern Canada to the northern states of Mexico (A.O.U., 1957).

TABLE 1
SCHEME FOR DETERMINING FAT CLASSES IN *ZONOTRICHIA LEUCOPHRYS ORIANTHA*
BY APPEARANCE OF FAT DEPOTS

| Fat class | Fat depots and appearance with respect to fat | | |
|-----------|---|---------------------------------------|--|
| | Claviculocoracoid | Lateral thoracic, subalar, and spinal | Medioventral, abdominal, and ischiopubic |
| 0 | None | None | None |
| 1 | None | Streaks | Streaks |
| 2 | Trace | Partially filled | Thin covering |
| 3 | Partially filled | Prominent, filled | Thick covering |
| 4 | Filled flush | Bulging | Bulging slightly |
| 5 | Bulging | Bulging | Bulging |

METHODS

This study was conducted for three consecutive summers from 1968 to 1970 near Tioga Pass, Mono County, California. The study area contained many wet, sub-alpine meadows between altitudes of 2,896 and 3,140 m (9,500–10,300 feet) that were occupied by *Z. l. oriantha*. Field work started in early June in 1968 and 1969 and in late May in 1970. We camped at the study area and worked continuously throughout all three summers until the last week in September.

Birds were collected with gun, trap, or net and weighed to the nearest 0.1 g. Those retained for fat extraction were stored in a freezer at Lee Vining, California, and taken later to the laboratory under dry ice. Those released were banded with Fish and Wildlife Service bands. Sex was determined in released birds by the presence of a cloacal protuberance or brood patch in breeding adults and by laparotomy in postbreeding adults and immatures. We noted that birds tended to lose about 0.3 g in the 24-hour period following laparotomy. By the third day they were back to their prelaparotomy weight. Therefore in our analysis of body weights we excluded weights obtained within 3 days after laparotomy.

In the course of the three summers of work we captured, banded, and released 138 adult males, 107 adult females, 184 immature males, and 148 immature females. From this group we made 360 recaptures of adult males, 174 of adult females, 706 of immature males, and 497 of immature females. Within a given summer the number of recaptures of specific individuals ranged from none to as many as 26.

Total body lipids were obtained by extracting them from the carcass, minus the gonads, with petroleum ether for 24 hours in a soxhlet apparatus. The lipid thus obtained has been expressed in terms of a lipid index, which is the percentage of total body weight consisting of ether-extractable lipid.

Using the description of fat depots in *Z. l. gambelii* by McGreal and Farner (1956) and King and Farner (1965) as a guide, we devised a scheme for designating the state of obesity in live birds. They were inspected visually and assigned to fat classes from 0 to 5 according to the appearance of several key depots (Table 1). In our scheme we relied heavily on the appearance of the claviculocoracoid depot when making the decision on fat class. Fat class can be converted into approximate lipid index values by consulting Table 2, which shows the relationship between fat class and lipid index in 81 birds we examined for fat class prior to extraction.

In the summers of 1969 and 1970 some *Z. l. oriantha* captured during the first half of July were kept in captivity at our camp and weighed three times per week.

TABLE 2
RELATIONSHIP BETWEEN LIPID INDEX OF *Z. L. ORIANTHA* AND FAT CLASS

| | Fat Class | | | | | |
|--------------------|-----------|------|------|-------|-------|-------|
| | 0 | 1 | 2 | 3 | 4 | 5 |
| Mean lipid index | 2.55 | 4.19 | 6.27 | 11.38 | 14.77 | 20.43 |
| Standard deviation | 1.07 | 2.08 | 2.01 | 3.88 | 4.40 | 4.72 |
| N | 14 | 24 | 15 | 8 | 10 | 10 |

They were held two per cage (cages were $30 \times 21 \times 20$ cm) in a 4.5×4.5 m tent with mesh windows or doors on all four sides. Thus the birds were exposed to natural oscillations in temperature and photoperiod. Water in bottles and food in the form of commercial game bird mix and mixed seed were provided ad libitum.

Every year we captured some *Z. l. gambelii* on the study area. They were, no doubt, in transit between their breeding grounds in Canada or Alaska and wintering areas that could be valleys flanking the Sierra or beyond them to the south. Members of this race first appeared at Tioga Pass, as indicated by our trapping records, on 12 September 1968, 12 September 1969, and 11 September 1970.

RESULTS AND DISCUSSION

Our field work did not begin early enough in any year for us to determine the *Z. l. oriantha* population's exact schedule of arrival, but males tended to arrive ahead of females and most of the population arrived during late May. Egg-laying began in early June and ended in mid- or late July. Weather conditions modified the schedule slightly from year to year. Postnuptial molt generally began before nesting activities ended, but individuals did not begin to molt until after their young had fledged.

Our data are few on this point, but females apparently arrived at the breeding ground with considerable lipid stores as indicated by their body weights and fat classes (Figure 1). Their weights decreased briefly following arrival and then began to increase during the nesting period until they equaled or exceeded those of the much leaner males. Individual histories showed that this increase in body weight of females began at the time of ovogenesis and that visible fat stores were maintained through incubation. We do not know the physiological or behavioral basis for this accumulation and retention of fat. Perhaps the energetic cost of incubation in wild birds is not so great as that found in captives (Kendeigh, 1963; El-Wailly, 1966; Brisbin, 1969). Another possibility is that wild birds, functioning within a greatly different array of stimuli than captives, are stimulated to eat more than captives during incubation. Retaining fat during incubation may have numerous advantages, considering especially the relatively short nesting season at high

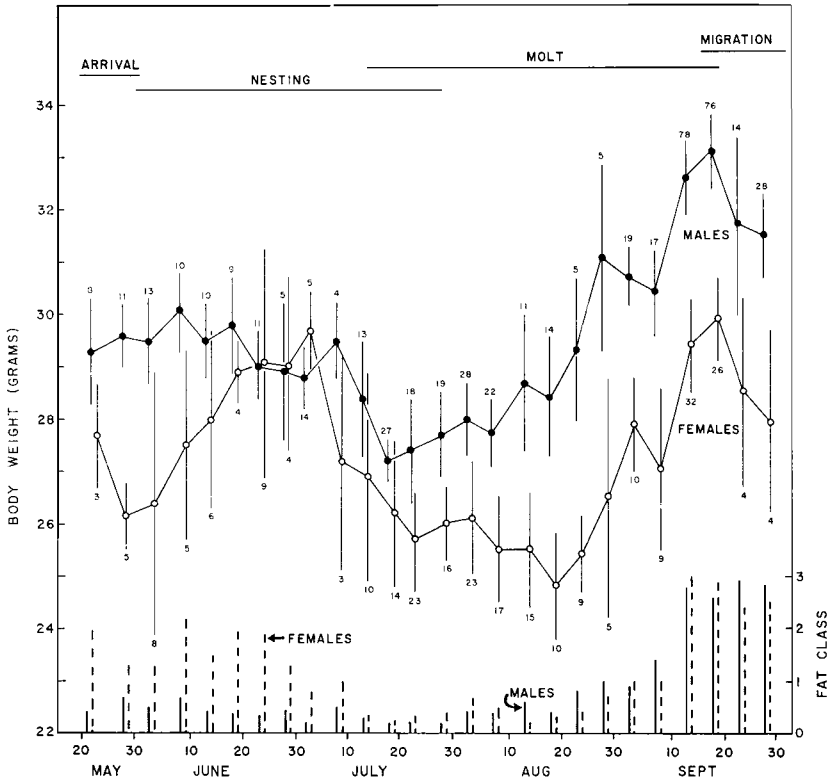


Figure 1. Mean body weights, fat classes, and chronology of events on the central Sierra Nevada breeding grounds for adult *Zonotrichia leucophrys oriantha*. Means for weight and fat data are given at 5-day intervals. Vertical lines denote ± 2 SE of mean for body weights. Numerals indicate sample size for body weights and for the concurrent plot of fat class.

altitude. If snowstorms prevent access to food for a day or so, females should be able to continue incubating successfully while males move temporarily to feed at lower elevations. Fat reserves could also be important in minimizing the time required for renesting if a clutch is lost from predation.

Mean body weights began to decrease in both sexes in early July. This was correlated with their care of young. The mean total weight loss was 7.8 percent in males and 12.8 percent in females. These losses resemble closely those reported in other small passerines at the same phase of the reproductive cycle (Heydweiler, 1935; Nice, 1937; Newton, 1966). Males tended to recover their losses after mid-July whereas the females did not. We feel that this was probably due to the greater role

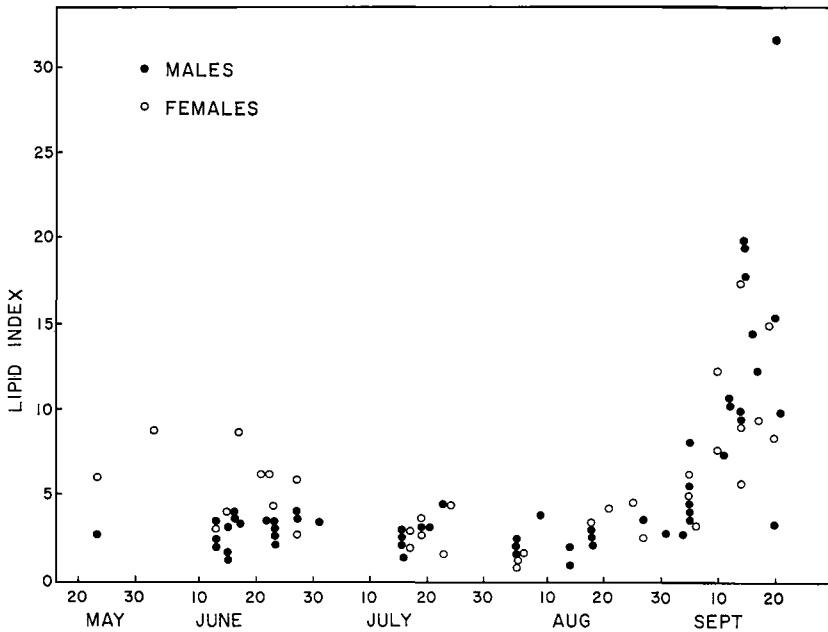


Figure 2. Lipid indexes for 56 adult male and 34 adult female *Zonotrichia leucophrys oriantha* collected on their breeding grounds in the central Sierra Nevada.

females played in feeding young after they left the nest. Females usually fed their young and traveled with them for about 2 weeks after fledging. Males fed chicks regularly in the nest, but only sporadically after they fledged. King et al. (1965) report essentially this same pattern of weight fluctuations in adult birds, but with less amplitude, during the first part of the summer in *Z. l. gambelii* breeding in central Alaska.

Our data on total extractable lipids in *Z. l. oriantha* during breeding season suggest that some females were relatively fatter than males in the early summer and that a marked increase in extractable lipid occurred in both sexes prior to migration (Figure 2). Body weight and lipid reserves, as manifested in fat class, increased in both sexes during the last half of the postnuptial molt. As individuals fattened to fat class 3 or above, they left the breeding grounds. This departure of fattened birds is the reason for the decrease in mean body weight of resident birds caught in late September and for the decrease in the number of individuals captured at that time (see Figure 1). The large increase in sample size in mid-September was probably due to decreased trap-wariness associated with premigratory hyperphagia.

The relationship of premigratory fattening to molt is illuminated fur-

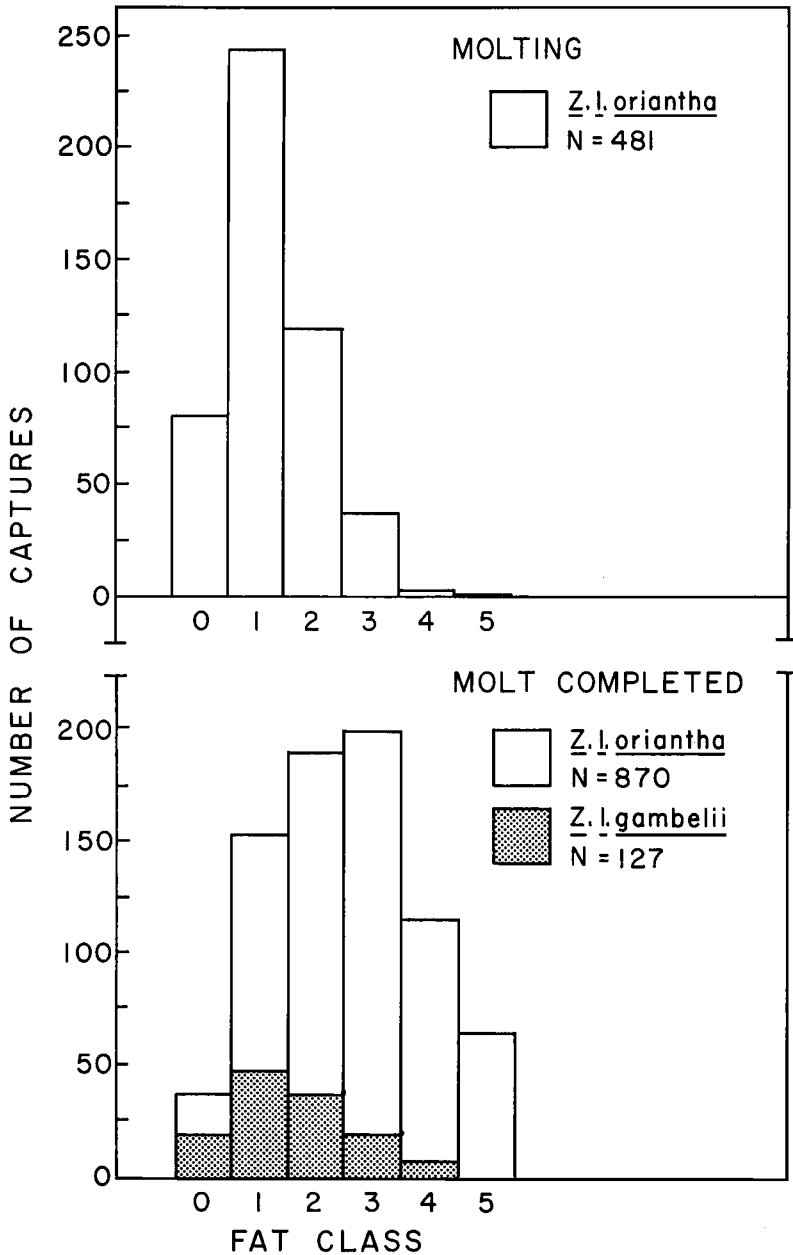


Figure 3. Fat classes of molting and nonmolting *Zonotrichia leucophrys oriantha* captured in September at Tioga Pass. Also shown are fat classes of intramigratory *Z. l. gambelii* captured in September at Tioga Pass.

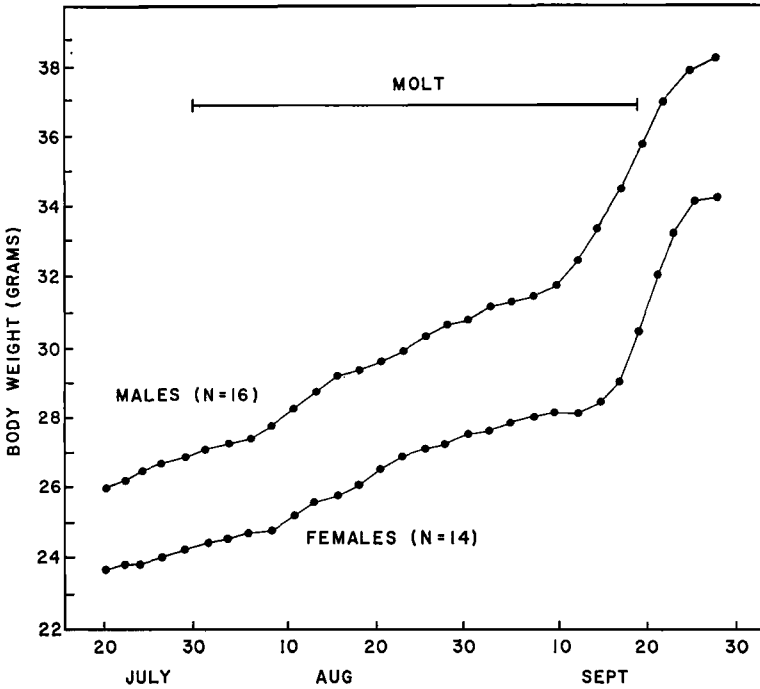


Figure 4. Mean body weights and the period of molt in captive adult *Zonotrichia leucophrys oriantha*.

ther by comparing fat classes of molting and nonmolting birds captured late in the summer (Figure 3). Of 481 September captures of molting birds, 91.7 percent were class 0-2 and 8.3 percent were class 3-5. Of 870 September captures whose molt was completed 43.6 percent were class 0-2 and 56.4 percent were class 3-5. Molting birds generally had some visible fat, and many deposited large quantities before molting ceased. A substantial amount of fattening also occurred between the end of molt and the start of migration. Individuals retrapped during this interval gained an average of 1.2 g/day in body weight.

In general the nonfat body components of small birds are homeostatic and changes in body weight are due principally to changes in fat stores (Odum, 1958, 1960, 1965; Odum et al., 1964). Caution is warranted, because nonfat components may be catabolized once fat stores are depleted (Odum et al., 1964; King et al., 1965; Johnston, 1968). The fat-free body weight of *Z. l. oriantha* used in fat extractions was 28.27 ± 1.41 g for 56 males and 25.47 ± 1.58 g for 34 females. If we assume these figures are valid for the birds ready to migrate we can calculate

from body weights alone that the average premigratory lipid index on 18 September was 14.2 for males and 15.0 for females. This is consonant with our data on total extracted lipids from birds taken about that time (see Figure 2).

In captive adult *Z. l. oriantha* body weight increased slowly but steadily in both sexes through the period of postnuptial molt and then increased much more rapidly just before the end of molt. At their terminal weight all birds were fat class 4 or 5 (Figure 4). These weight records of captives have been normalized by using the day when molt began as a common reference point for body weights. As the start of molt ranged over 17 calendar days during the 2 years, the abscissa in Figure 4 is slightly inaccurate for most of the birds, but the trends are represented faithfully.

As in the wild population, males were heavier than females. The rate of weight gain during most of the molt period was about 0.1 g/day for both sexes. The final, more rapid gain occurred at an average of about 0.5 g/day, but individuals often gained about 1.0 to 1.5 g/day for a few consecutive days during the final fattening phase. Thus they displayed about the same rate of fattening seen in retrapped members of the wild population during their most active period of weight gain.

This pattern wherein energy is apparently partitioned between storage and utilization for feather growth is quite different from the pattern of autumnal premigratory fattening in *Z. l. gambelii*. In that race no indication of fattening was detected prior to the end of postnuptial molt (King et al., 1965). And even beyond the period of molt only a slight amount of fattening occurred, and they apparently began the southward migration with low fat reserves (7 to 8 percent of total body weight).

Our estimates of fat class in transient *Z. l. gambelii*, using the same criteria as for *Z. l. oriantha*, indicate that *Z. l. gambelii* left our trapping area before becoming extremely obese (see lower portion of Figure 3). Of 127 captures, 80.3 percent were class 0-2 and 19.7 percent were class 3-5. Retrapped individuals fattened at the rate of 0.3 g/day at Tioga Pass. The mean lipid index was 5.1 for 3 adult females and 2 adult males captured 25 September 1970 at Tioga Pass.

It is difficult to generalize about the energetic strategies employed by avian species during autumn migration. The magnitude of fattening may vary interspecifically or even intraspecifically, and with the stage of migration. For example, Dunlins (*Erolia alpina*) have fat reserves amounting to about 10 to 15 percent of body weight before leaving the breeding grounds (Holmes, 1966; Yarbrough, 1970), but reserves may account for 40 percent of body weight in transients (Mascher, 1966). Passerines intercepted during autumn migration along the Baltic coast

usually have moderate to heavy fat reserves, but the data are difficult to interpret as the degree of fatness may vary with distance from the breeding area (Dolnik and Blyumental, 1967). Caldwell et al. (1964) have suggested that in overland and southbound migrants fat reserves increase during each stop and reach a maximum level as the birds initiate long overwater flights at the Gulf Coast.

Other variables that affect fatness in migrants include the effects of previous flights, weather conditions, and handling by the investigator (Mueller and Berger, 1966). Latitudinal effects, such as those seen in Chaffinches (*Fringilla coelebs*) may also play a role because in northern breeding populations migration occurs while the molt is in progress and is concurrent with the inception of fattening. In the southern populations on the other hand, molt, fattening, and migration are separate sequential events (Dolnik and Blyumental, 1967).

These three factors, molt, fattening, and sustained periods of flight can be identified as the primary events affecting energy balance in both spring and fall migration. Apparently there are no strict requirements as to how these factors interdigitate temporally. They may overlap considerably or be totally separated; it depends upon the species or even population in question.

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SUMMARY AND CONCLUSIONS

The seasonal changes in lipid reserves of *Z. l. oriantha* on their breeding grounds in the central Sierra Nevada of California were studied. Females had greater fat stores than males from the time of arrival through the time the young were hatched. The reserves of females were depleted while they fed young in the nest and for about 2 weeks post-fledging. The mean weight loss of females during this period was 12.8 percent. Loss in males was 7.8 percent. Males probably expended less energy than females in caring for fledglings. Both sexes deposited fat during postnuptial molt.

Both sexes showed an average weight gain of about 20 percent from the summer low to the autumn high. Total lipids, as judged by body weight and lipid extractions, averaged about 15 percent at the time of migration. This is about the magnitude of reserves seen in intracontinental migrant finches in the spring. Thirty adult birds held captive

during the summer at the study area showed a total weight gain of about 48 percent. Both captive and wild birds began gaining weight during the postnuptial molt. Fattening occurred more rapidly after molt was completed. This may have happened because of a shift in energy resources from feather growth to lipogenesis or because of an increase in appetite at that time.

In comparison to *Z. l. gambelii*, *Z. l. oriantha* are relatively obese when they initiate autumn migration. Perhaps these subspecies employ different energetic strategies in autumnal migration. This is not surprising. The energetic problems associated with migration must be quite different among migrants, and it seems unlikely that their solutions to these problems are identical.

The extent of autumnal premigratory fattening in *Z. l. oriantha* is comparable to that of vernal premigratory fattening in many species. The response probably involves an increase in appetite that is accurately timed. This is contrary to most current descriptions of autumnal premigratory fattening. We do not think that this is because *Z. l. oriantha* is unique. Undoubtedly other migrants act in the same way, but this will only be resolved when more data are collected on migrants on their breeding grounds.

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