

BODY COMPOSITION OF CAPTIVE WHITE-CROWNED SPARROWS DURING POSTNUPTIAL MOLT

JOHN D. CHILGREN

ABSTRACT.—A five-compartment analysis of body composition was performed on indoor and outdoor captive White-crowned Sparrows before, during, and after their postnuptial molt. Body weight was monitored simultaneously in four experimental groups. The duration of postnuptial molt in indoor and outdoor birds averaged 60 days. The body weight of outdoor captives in Pullman changed similarly to that seen during the early stages of molt in Fairbanks captives, although late molt autumnal fattening is less intense and more irregular in Pullman captives. Birds on a constant photoperiod at 5° and 15°C exhibited early weight gains, but these gains were either unsustainable or converted to weight losses as molt progressed.

Total body water in lean birds averaged 70% during molt and 68% after molt. The absolute weight of body water as well as body weight increased during molt. Thus the fractional TBW was essentially unchanged.

The stability of the plumage-free lean body mass during molt reflected the negligible extent to which body protein is catabolized, although nocturnal protein degradation was not examined. The lean body weight during molt averaged 23.8% of the lean wet weight, plumage free, or about 5.6 g, but both these figures were only slightly higher after the molt.

Plumage weight during the molt increased about 30%. Body feathers constituted the largest fraction (ca. 75%) of the plumage mass, even during molt. Plumage weight after molt was about 24% of the lean dry weight.

Body lipid reached its nadir at the onset of molt in Fairbanks captives ($LI = 3.5$), but increased 6- to 7-fold at the end of molt ($LI = 20$). In Pullman outdoor captives, the increment was about 5-fold. Indoor captives vary in postmolt fattening, depending perhaps upon prior photoperiodic history before transfer to a constant photoperiodic environment. Thus some individual birds transferred later in the spring showed some degree of postmolt fattening, whereas those transferred earlier showed none. This is but a tentative conclusion.

Although lipid reserves in the White-crowned Sparrow are small at the onset and perhaps most critical period of molt, the long feeding period and the mutual exclusion of the breeding and molting schedules preclude any apparent calorific drain on the avian body. It is suggested that the rapid molt period may be a selective force operating to separate temporally two events of the annual cycle that are potentially costly energetically.—*Department of Zoology, Washington State University, Pullman, Washington 99164. Present address: Department of Zoology, Oregon State University, Corvallis, Oregon 97331. Accepted 26 January 1976.*

THE YEARLY cycle of all passerines includes an annual molt, which usually begins after breeding or during its later stages. The Gambel Sparrow, *Zonotrichia leucophrys gambelii*, a member of the west coast complex of North American White-crowned Sparrows, molts after the cessation of all breeding activities while on its Alaskan and Canadian breeding grounds (see Cortopassi and Mewaldt 1965, for the distribution of this species), and has been reported to complete its postnuptial molt in 7 weeks (Morton et al. 1969), although this may be subject to some year-to-year variation (Chilgren 1975). In several passerines studied, the molt is usually characterized at some point early in the sequence by an increase in body weight (King et al. 1965, Newton 1968, Myrcha and Pinowski 1970, Morton and Welton 1973), suggesting that the molt does not exact a physiological hardship upon the animal, as might be expected in these birds that molt within 2 months. But body weight is not an appropriate index of the physiological impact of molt, and may mask the potential nutritional stress of a molt. Thus increases in body water, for example, may appear concurrently with decreases in body lipid or protein with little or no change in the bird's live weight or energy reserves. Only a few studies of molt have examined the

TABLE 1
MOLT STAGE CHARACTERISTICS DURING POSTNUPTIAL MOLT IN THE
WHITE-CROWNED SPARROW

Molt Stage	Characteristics
0	Before onset of molt
1	Primaries 1-4 and spinal tract molting
2	Primaries 5-7, tertials, thoracic, capital, and spinal tracts molting
3	Primaries 8-9, secondaries, femoral, and crural tracts molting
4	Primary or secondary molt completed
5	Body molt completed

concurrent variations of body composition (Newton 1968, Myrcha and Pinowski 1970, Gavrilov and Dolnik 1974). Although the lipid and fat-free weights of captive and free-living White-crowned Sparrows have been previously investigated (King et al. 1965), this analysis did not include alterations in body weight, lean dry weight, and plumage weight. The purpose of this study was to determine the body compositional changes in the White-crowned Sparrow by performing a five-compartment analysis before, during, and after postnuptial molt. An investigation of the energy costs of molt was conducted simultaneously and will be reported elsewhere. Molt can be induced photoperiodically out of season in *Z. l. gambelii*, like other aspects of its annual cycle (see Farner 1964, Farner and Lewis 1971), and hence can be studied at almost any time of the year.

MATERIALS AND METHODS

Migrant birds were trapped in central and eastern Washington and maintained in aviaries at Washington State University in Pullman (46°46'N) and at the University of Washington in Seattle. Individuals of group CP (24 females) were transferred on 28 May 1972 each to a small cage (41 × 28 × 25 cm) and placed outdoors in a Pullman aviary that shielded them from direct radiation, but only partly from wind. Thirty birds of undetermined sex were similarly caged and placed in constant temperature rooms at 5°C (group E5) and at 15°C (group E15). Another group, E25, composed of 6 birds held within a 25°C constant temperature room, were not analyzed for changes in body composition, but their body weights were monitored throughout molt.

Illumination consisted of eight 40-watt bulbs in each room, with a 16L:8D (light:dark) photoperiod. Water and a chick-starter mash were provided freely. Six birds trapped late in June 1973 near the University of Alaska in Fairbanks (64°50'N) before molt had begun were sacrificed, weighed, and frozen for later analysis. Eight other birds trapped in mid-June were used for metabolism studies; these were individually caged within a screened outdoor shelter and sacrificed for analysis after the molt. These 14 birds constituted group CF, but no body compositional analysis was performed on them during the molt itself, whereas birds belonging to other groups were analyzed at four different stages of molt as well as before and after molt. The molt stage characteristics are shown in Table 1. Only birds arbitrarily pre-selected for stage 5 from all groups were weighed to the nearest 0.1 g at least every other day throughout the molt. A bird at an appropriate molt stage was sacrificed about 2 h after the end of its natural or experimental day. The digestive tract was then flushed with air and weighed to the nearest 0.01 g.

Feathers were rapidly plucked and distributed into four classes: molting and nonmolting body feathers (including crown, wing, and tail coverts), and molting and nonmolting remiges and rectrices. Feathers were weighed to the nearest 0.1 mg and dried under vacuum for 24 h at 40°C (see Barnett 1970). The final weight of all feathers combined gave the dry plumage weight (DPWt) and plumage water (PW) by difference. Plucked carcasses were sealed in plastic bags and frozen for later analysis. Incisions in the abdominal, pectoral, and dorso-lumbar regions were made in partially thawed birds, which were then lyophilized for 4 days to remove carcass water, the latter calculated by difference in body weight. To this value was added plumage water to obtain the total body water (TBW). The gizzard of a desiccated bird was removed and dissected to remove any undigested food. The weight of the material present was subtracted from the live body weight to obtain the true wet body weight. The carcass was then ground with a mortar and pestle, and as much of the homogenate as possible was placed in a tared cellulose

extraction thimble and weighed. Residue in the mortar was accounted for in the final calculation. Lipid was extracted with diethyl ether for 24 h in a Soxhlet apparatus. Feather lipid was not extracted, but was assumed negligible on the basis of its low relative proportion, being about 1% of the feather wet weight (Penney and Bailey 1970). The lipid-free carcasses in the thimbles were oven dried at 70°C for 24 h and reweighed. Water loss from the thimbles themselves was corrected for. The residue was the dry fat-free carcass weight (DFFCWt). To this was added the plumage weight to obtain the total dry fat-free body weight (DFFBWt) or lean dry weight. Total lipid, plumage water, body water, plumage weight, and lean dry weight were then calculated on absolute and relative bases. Tests of significance were based on a 1-tailed Student's *t*-test, with the level of significance fixed at 5%. Means given in the text are followed at all times by the standard deviation.

RESULTS AND DISCUSSION

Any valid comparison of variables among the different experimental groups demands that the tempo and duration of molt among the groups be similar. All four groups resembled one another in the duration of molt of primaries, secondaries, and other major feather groups, although the body molt and hence the complete molt was protracted in group E15 (67.4 ± 3.7 days) and shortened in group E5 (54.3 ± 3.7 days $P < 0.001$). The body molt in its later stages had no impact upon the present study, as it involved only a few sparsely distributed feathers. Both outdoor groups (CP and CF) averaged near 60 days to complete the molt.

Body weight.—Contrary to earlier observations (King et al. 1965), the body weight changes in Pullman captives during the first half of postnuptial molt resembled, at least superficially, those of free-living birds or captives at Fairbanks. Thus, groups CP, E5, E15, and E25 all showed increases in body weight in the first 2–3 weeks of molt, although in the indoor groups it was not sustained (compare Fig. 1B with Fig. 1A, 1C, and 1D). Mean body weight changes in group CP were highly variable, correlating in part with variable climatic conditions, but nevertheless displayed characteristic increases in body weight in the last week of molt. Although Pullman captives do not migrate or breed and the onset of molt is less precise than it is in Alaskan birds, the molt spans the calendar period of time occupied by the molt in feral birds whether captured as adults that had presumably bred, or as young that had no breeding history. Thus it appears that photoperiodic influences at higher latitudes serve to sharpen the timing of light-dependent responses, such as molt, and that prior breeding or migratory experience is not essential for the expression of a normal postnuptial molt.

Rather than phasing the onset of molt in groups E5 and E25 to the same day, as was done for group E15 (see Fig. 1), I compared groups E5 and E25 on a calendar basis as they were caged only one day apart, and were all captured near Pullman. Thus temperature appeared to be the only conspicuous variable, except for different numbers of birds in each room. Presented in this fashion, the mean body weight changes are more variable as all birds are never in the same phase of molt, but basic body weight trends are not altered. The most apparent contrast between Figure 1C and 1D is the difference in mean time of molt onset, which occurred about 12 days earlier in group E25 (compare June 18 ± 3.7 days with June 30 ± 5.1 days). The only comparable data are those of Blackmore (1969) whose study of molt in the House Sparrow (*Passer domesticus*) suggested that low temperature (3°C) inhibited and high temperature (32°C) induced molting, supporting the above observations.

Furthermore the molt in group E5 was about one week shorter ($P < 0.05$) than that in group E25, which could not be accounted for on the basis of molt duration in

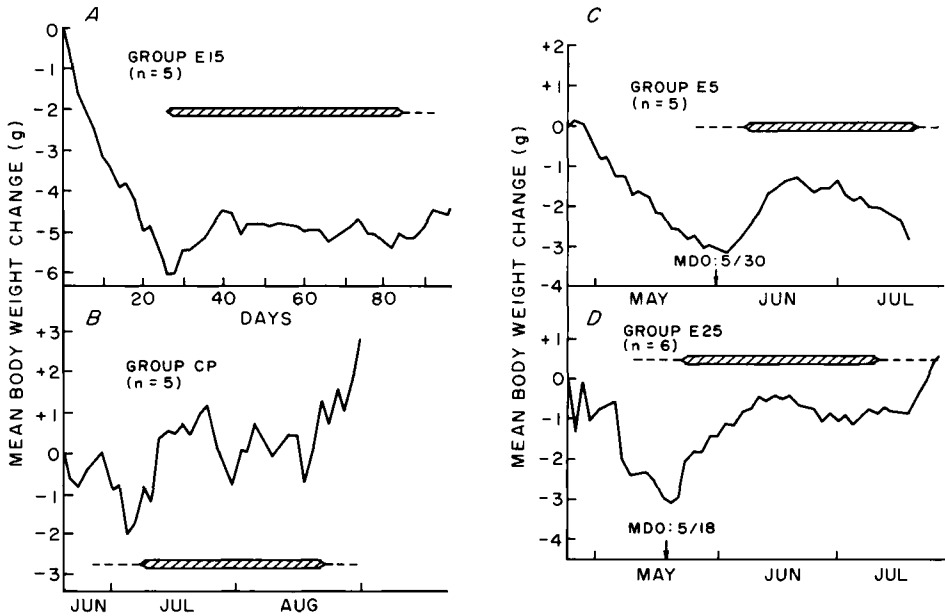


Fig. 1. Mean variations in body weight of captive White-crowned Sparrows at Pullman. The shaded bars show the period of molt. A, indoor captives at 15°C; B, outdoor captives; C, indoor captives at 5°C; D, indoor captives at 25°C. The MDO in C and D is the mean day of onset of postnuptial molt (month/day).

individual feather tracts. Apparently the interval between onset of molt in feather groups was compressed in group E5, but it is tempting to suggest a physiological basis for the shorter molt period. As a compensatory response to a cool environment while the plumage is developing and whole-body conductance is elevated (Chilgren 1975), a shorter molt period would reduce the total energy expenditure required.

Finally, the body weight of group E5 diminished toward the end of molt, unlike that of group E25, which also showed postmolt increases that were smaller and delayed if compared with groups CP or CF (Figs. 1B and 2). Whether further increases in body weight would have been observed in group E5 had the measurements extended into the postmolt period is unanswerable, but with the data available, it seems likely that any increases would be of small magnitude.

Body water.—Total body water (TBW) includes water within and absorbed upon feathers as well as internal body fluid water. Absorption water contributed least to the TBW, being about 6% of the total plumage weight and between 0.05 and 0.06% of the TBW. The TBW fraction was largest in group CF (Table 2 and Fig. 3B), amounting to 18 g or 68% of the body weight at stage 0. Thus TBW in *Z. l. gambelii* conforms to the value of 67% reported in an earlier study of the composition of the avian body (Turček 1960), and approximates that found in small mammals (Gorečki 1965). More recent investigations of North American birds reinforce Turček's estimate of body water. Thus the body water as a fraction of the lean wet weight is 69–70% in the Dickcissel, *Spiza americana* (Zimmerman 1965), 67% in the Junco, *Junco hyemalis* (Helms et al. 1967), 66.5% in the White-throated Sparrow, *Zonotrichia albicollis* (Kontogiannis 1968), 68% in the Tree Sparrow, *Spizella arborea* (Helms and Smythe 1969), 64–65% in the Chaffinch, *Fringilla coelebs* (Gavrilov and Dilnik 1974), but only 60% in the Redpoll, *Carduelis flammea* (Newton 1969). In an equatorial bird, the Yellow-vented Bulbul, *Pycnonotus goiavier*, it is 67–68%

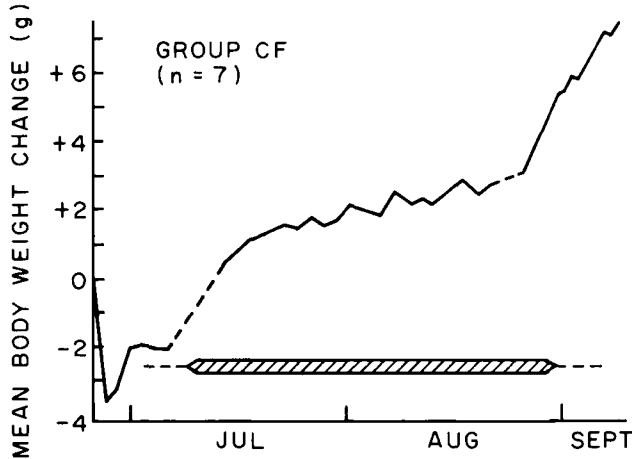


Fig. 2. Mean variation in body weight of outdoor captives at Fairbanks. The shaded bar shows the period of molt. The dotted portions of the line represent periods when no data were obtained.

(Ward 1969a). If the TBW of *Z. l. gambelii* is computed as a percentage of the lean wet weight rather than of the wet weight, the total body water fraction averages a consistent 68.5–71% during molt. Thus the mean percent of body water in lean birds of all experimental groups combined was 69.5 ± 0.79 , 70.8 ± 0.19 , 70.3 ± 0.17 , and $68.4 \pm 0.71\%$ for molt stages 1 to 4, respectively. After molt it was $67.8 \pm 1.13\%$ ($68.2 \pm 0.65\%$ if the all-female group CP is excluded from this computation).

In group CP the TBW increased slightly during the molt, but decreased to 53% of the live wet weight after molt (Table 2). Decreases in TBW occurred in both groups CP and CF between stages 0 and 5, at 5 and 8%, respectively. A similar pattern of TBW change was noted in groups E5 and E15, but with increases in TBW between stages 0 and 5, which were insignificant.

Plumage water within developing quills increased from 0 to about 0.75 g at the peak of molt. Total plumage water (PW), including adsorbed water, increased by more than five times from premolt values to stage 3, the assumed peak intensity of molt

TABLE 2
TOTAL BODY WATER (TBW) COMPOSITION AT DIFFERENT STAGES OF POSTNUPTIAL MOLT IN CAPTIVE WHITE-CROWNED SPARROWS

Molt stage	N	Group CP ^a	N	Group CF ^a	N	Group E5 ^b	N	Group E15 ^b
0	3	16.42 ± 1.45 ^c (64.40 ± 3.17)	6	18.00 ± 1.88 (68.16 ± 0.86)	4	16.00 ± 1.41 (61.44 ± 3.11)	3	14.49 ± 2.18 (51.70 ± 2.69)
1	3	15.34 ± 0.13 (66.68 ± 0.72)	—	—	3	15.86 ± 1.54 (64.18 ± 1.78)	5	16.66 ± 1.27 (66.80 ± 1.50)
2	4	16.12 ± 0.70 (66.97 ± 0.84)	—	—	4	18.18 ± 2.42 (67.91 ± 0.86)	4	16.85 ± 1.85 (66.80 ± 1.29)
3	5	16.79 ± 1.51 (65.91 ± 0.95)	—	—	5	18.07 ± 0.92 (66.65 ± 1.44)	5	17.47 ± 1.08 (66.59 ± 0.63)
4	4	15.57 ± 0.45 (64.46 ± 1.36)	—	—	3	15.72 ± 1.09 (61.26 ± 3.29)	4	15.33 ± 0.99 (66.90 ± 3.90)
5	5	15.61 ± 1.41 (53.00 ± 3.75)	8	16.56 ± 1.46 (53.88 ± 2.04)	5	16.59 ± 0.72 (65.12 ± 1.23)	4	15.46 ± 0.75 (56.08 ± 5.50)

^a Caged outdoors. ^b Caged indoors. ^c Mean (g) ± standard deviation (percentage of whole wet weight in parentheses).

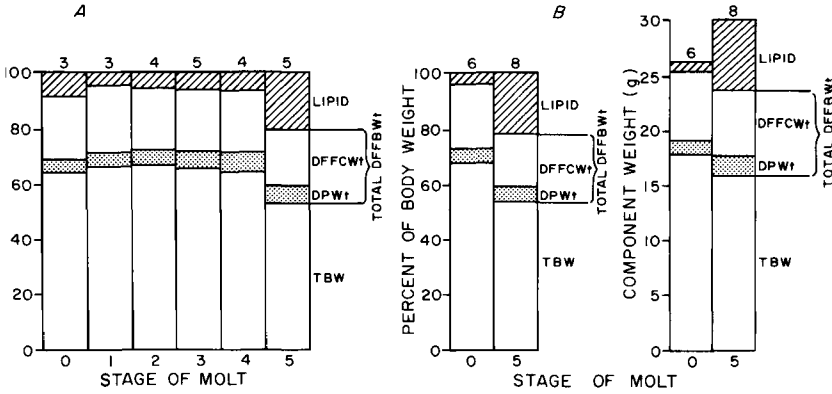


Fig. 3. A, variation in mean percentage weight of body components before, during, and after postnuptial molt in outdoor captives at Pullman (group CP). B, variation in mean percentage and measured weight of body components before and after postnuptial molt in outdoor captives at Fairbanks (group CF). Number of birds per stage given at the top of each bar.

(Table 3). Not all of the body water increment during molt could be attributed to increased plumage water. Because percentage as well as absolute TBW increased in all groups measured between stages 0 and 3, the extracellular fluid volume probably increased as well, as supporting data indicate (Chilgren and deGraw MS).

Dry fat-free body and carcass weights.—These two components comprise the fat-free dry mass with and without the plumage, respectively, the latter being the least variable of components analyzed (Table 4; Figs. 3 and 4). Absolute mean values of the lean dry carcass weight (DFFCWt) varied no more than 0.56 g in any single group of birds between any two stages of molt, and the largest relative change was less than 4% in any one group. The means of the DFFCWt averaged throughout molt stages 1 to 4 were 5.45 ± 0.14 , 5.76 ± 0.23 , and 5.68 ± 0.17 g for groups CP, E5, and E15, respectively. If expressed as a percentage of the lean wet carcass weight rather than the total wet weight, as in Table 4, the DFFCWt averages about 23.8% at any molt stage (group CP: 23.8 ± 0.54 ; group E5: 23.9 ± 1.36 ; group E15: 23.7 ± 0.31), but is probably larger in free-living birds as the fat-free body weight in

TABLE 3
WEIGHT OF PLUMAGE WATER (PW) AT DIFFERENT STAGES OF POSTNUPTIAL MOLT IN CAPTIVE WHITE-CROWNED SPARROWS

Molt stage	N	Group CP ^a	N	Group E5 ^b	N	Group E15 ^b
0	3	0.17 ± 0.09^c (0.66 ± 0.39)	4	0.15 ± 0.01 (0.48 ± 0.22)	3	0.16 ± 0.08 (0.65 ± 0.27)
1	3	0.42 ± 0.05 (1.82 ± 0.22)	3	0.19 ± 0.04 (0.82 ± 0.23)	5	0.46 ± 0.20 (1.69 ± 0.75)
2	4	0.70 ± 0.14 (2.88 ± 0.57)	4	0.76 ± 0.23 (2.76 ± 0.62)	4	0.50 ± 0.27 (2.30 ± 0.62)
3	5	0.90 ± 0.20 (3.49 ± 0.55)	5	1.00 ± 0.20 (3.67 ± 0.66)	5	0.84 ± 0.60 (3.18 ± 0.18)
4	4	0.27 ± 0.12 (1.13 ± 0.46)	3	0.12 ± 0.06 (0.81 ± 0.20)	4	0.22 ± 0.05 (0.98 ± 0.10)
5	5	0.12 ± 0.01 (0.50 ± 0.56)	5	0.19 ± 0.04 (0.76 ± 0.20)	4	0.16 ± 0.05 (0.64 ± 0.12)

^a Caged outdoors. ^b Caged indoors. ^c Mean (g) ± standard deviation (percentage of whole wet weight in parentheses).

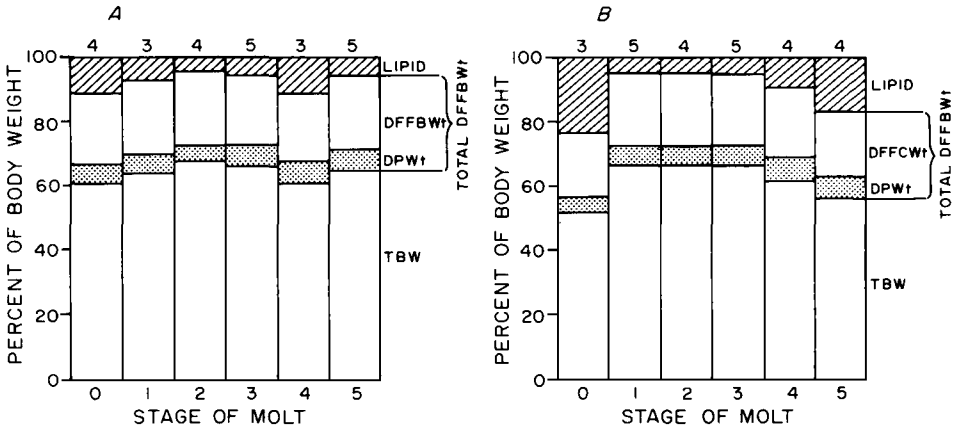


Fig. 4. Variation in mean percentage weight of body components before, during, and after postnuptial molt in A, 5°C-acclimated (group E5) and B, 15°C-acclimated (group E15) indoor captives.

captives held in small cages averages about 1 g less than in free-living birds (King 1961). This is also suggested by the higher DFFCWt of group CF as compared with groups E5 and E15, especially at molt stage 0. After molt the ratio of DFFCWt to lean wet weight ($\times 100$) is $24.5 \pm 0.81\%$ for all four groups analyzed, indicating that body ash and protein represent nearly a quarter of the lean weight. In freshly molted birds, the DFFCWt is about 20–21% of the total wet weight, corresponding to about 5.6–5.7 g. During the molt these values are slightly higher at about 22% and 5.75 g.

The combined weight of plumage and dry fat-free carcass weight, forming the total lean dry weight (DFFBWt), parallels changes in the DFFCWt, and is about 7 g after molt in the all-female group CP, but is higher in the predominantly male group CF, at about 7.7 g (Table 2).

The stability of the lean carcass weight suggests that protein degradation does not accompany molt in the White-crowned Sparrow. In contrast, Canada Geese (*Branta canadensis*) undergo a marked reduction in the mass of the pectoral muscles, although metabolizable fat is only partially utilized (Hansen 1962). In the Chaffinch the lean dry weight also decreases by about 1 g during molt but recovers after molt

TABLE 4
DRY FAT-FREE CARCASS WEIGHT (DFFCWt) AT DIFFERENT STAGES OF POSTNUP TIAL MOLT IN CAPTIVE WHITE-CROWNED SPARROWS

Molt stage	N	Group CP ^a	N	Group CF ^a	N	Group E5 ^b	N	Group E15 ^b
0	3	5.67 ± 0.43 ^c (22.27 ± 1.46)	6	6.18 ± 0.56 (23.26 ± 0.33)	4	5.83 ± 0.41 (22.38 ± 0.97)	3	5.55 ± 0.74 (19.32 ± 1.04)
1	3	5.43 ± 0.23 (23.83 ± 1.11)	—	—	3	5.76 ± 0.40 (22.95 ± 0.61)	5	5.80 ± 0.31 (22.87 ± 0.45)
2	4	5.37 ± 0.26 (22.26 ± 0.70)	—	—	4	6.02 ± 0.71 (22.19 ± 0.90)	4	5.70 ± 0.43 (22.64 ± 0.48)
3	5	5.66 ± 0.40 (22.16 ± 0.91)	—	—	5	5.81 ± 0.27 (22.52 ± 0.48)	5	5.79 ± 0.35 (22.06 ± 0.40)
4	4	5.33 ± 0.21 (22.07 ± 0.67)	—	—	3	5.46 ± 0.48 (21.26 ± 1.23)	4	5.43 ± 0.43 (21.50 ± 0.77)
5	5	5.38 ± 0.50 (20.59 ± 1.42)	8	5.97 ± 0.48 (19.34 ± 1.27)	5	5.74 ± 0.23 (22.14 ± 0.68)	4	5.55 ± 0.25 (20.19 ± 2.26)

^a Caged outdoors. ^b Caged indoors. ^c Mean (g) ± standard deviation (percentage of whole wet weight in parentheses).

TABLE 5
PLUMAGE WEIGHT (PWT) AT DIFFERENT STAGES OF POSTNUPTIAL MOLT IN
CAPTIVE WHITE-CROWNED SPARROWS

Molt stage	N	Group CP ^a	N	Group CF ^a	N	Group E5 ^b	N	Group E15 ^b
0	3	1.20 ± 0.23 ^c (4.75 ± 1.03)	6	1.33 ± 0.99 (5.09 ± 0.61)	4	1.50 ± 0.20 (5.77 ± 0.97)	3	1.45 ± 0.08 (5.07 ± 0.22)
1	3	1.23 ± 0.14 (5.33 ± 0.54)	—	—	3	1.48 ± 0.01 (5.84 ± 0.86)	5	1.28 ± 0.11 (5.23 ± 0.39)
2	4	1.27 ± 0.19 (5.27 ± 0.59)	—	—	4	1.44 ± 0.16 (5.40 ± 0.44)	4	1.34 ± 0.13 (5.25 ± 0.18)
3	5	1.51 ± 0.10 (5.93 ± 0.63)	—	—	5	1.78 ± 0.16 (6.59 ± 0.69)	5	1.61 ± 0.22 (6.12 ± 0.65)
4	4	1.68 ± 0.10 (7.00 ± 0.42)	—	—	3	1.66 ± 0.03 (6.50 ± 0.51)	4	1.91 ± 0.14 (7.56 ± 0.50)
5	5	1.65 ± 0.08 (6.45 ± 0.51)	8	1.72 ± 0.13 (5.71 ± 0.25)	5	1.76 ± 0.13 (6.78 ± 0.41)	4	1.86 ± 0.05 (6.78 ± 0.89)

^a Caged outdoors. ^b Caged indoors. ^c Mean (g) ± standard deviation (percentage of whole wet weight in parentheses).

(Gavrilov and Dolnik 1974). For the many species of birds that molt flight feathers simultaneously (see Woolfenden 1967), growth of such a large number of feathers at once demands sufficient amino acid intake for feather synthesis. This is especially true of those essential or obligatory amino acids that cannot be manufactured de novo in the animal. In particular, the amino acid cystine may be a limiting factor if its precursor, methionine, is inadequately supplied by the diet. Cystine accounts for 6.4% and 6.9% of the total protein weight in goose and hen feathers, respectively (Block 1938). The beta-keratin of feathers therefore contains a greater amount of cystine than do most other proteins, which may have proportionately little or no cystine present (e.g. Tristram and Smith 1963). The data obtained in this study do not exclude the possibility of nocturnal protein degradation, as has been described in the Bullfinch, *Pyrrhula pyrrhula*, during its postnuptial molt (Newton 1968). Because of the long days available for feeding in July, the Gambel Sparrow is probably seldom stressed to the point of mobilizing structural protein for feather protein precursors. Nevertheless it may be of interest to determine if there is a correlation between latitude of breeding and extent of protein catabolism during molt in migratory passerines, as there is a strong correlation between molt duration and latitude of breeding in several species of birds (Morton et al. 1969, Chilgren 1975).

Plumage weight.—The dry plumage weight (DPWt) is the weight of dried molting and nonmolting feathers (Table 5). Although the plumage weight in captives may increase by as much as 40% in individual birds, the mean increase in feral birds may be closer to 30%, as demonstrated by Group CF. Indeed the mean increase of all groups between stages 0 and 5 is nearly 28% (1.37 ± 0.16 g to 1.75 ± 0.12 g). In all groups the body feathers, exclusive of wing and tail feathers, constitute 75% of the total plumage weight, even during the molt. The most intense period of molt should then coincide with the greatest number of body feathers in molt, but because feather tracts molt asynchronously, the potential severity of the molt is somewhat attenuated. Peak feather weight occurred at stages 3 or 4 when most feathers were molting. The wet weights of feathers at these stages commonly exceeded 2.5 g and therefore represented 10 to 12% of the total live wet weight of the bird. The DPWt following molt was 5.7 to 6.8% of the live weight, depending on the state of obesity. The dried plumage weight was 1.65 to 1.85 g in freshly molted birds, the male

plumage weighing about 4% more than that of the female. The dry plumage, as expressed as a percentage of the DFFBWt, averaged $19.1 \pm 1.73\%$ before molt in all groups, and increased to $24.5 \pm 1.36\%$ at stage 4. After molt it was $23.7 \pm 1.13\%$. This species must then produce nearly one-fourth of its lean dry body mass during the molt.

Feather weight was significantly greater ($P < 0.05$) following molt than before its onset in all groups, but there was no correlation between final DPWt and experimental condition, e.g. plumage weight in group E5 was not different from that of either outdoor group. The failure of cold ambient temperatures to induce a heavier plumage supports the results of Southwick (1971) who noted that different thermal indoor environments failed to elicit changes in the weight of the contour feathers in *Z. l. gambelii*. The potential for increased plumage weight apparently does exist, as he found a significant 19% increase in the weight of contour feathers of birds kept in outdoor aviaries in Pullman, whereas indoor captives subjected to 28°C, 4°C, or fluctuating air temperatures showed no seasonal differences.

The relationship of plumage weight to body weight is allometric. Turček (1966) examined the plumage weight of 91 species of birds with a weight range of nearly 2,000 g and formulated an expression for feather weight as a function of body weight: $F_w = 0.09 W^{0.95}$, where W is the body weight in grams. This indicates that in small birds the plumage weight is almost 9% of the body weight, but in the White-crowned Sparrow the plumage weight is only 6.7% of the body weight in lean birds (less in obese birds). This is not unexpected because the fringillids Turček examined are all partial migrants or resident birds, which are undoubtedly subjected to colder winter temperatures than are long distance migrants, such as *Z. l. gambelii*. One function of molt is to augment cold endurance. For example, the plumage of the House Sparrow, *Passer domesticus*, weighed up to 70% more after the molt, which accounts for its greatest cold tolerance at that time (Barnett 1970). Still its plumage weight after molt is only 7.5% of the lean body weight. The benefits accruing from a dense plumage in the Gambel Sparrow would be few, in contrast to birds wintering in colder regions (e.g. Berthold and Berthold 1971), as migrating to southern latitudes compensates, at least in part, for cold endurance at higher latitudes.

Body lipid.—Total ether-extractable fat in free-living birds was low at the onset of molt (Table 6, Fig. 3B), amounting to less than 1 g, an equivalent lipid index or LI (grams of fat per 100 g live weight) of about 3.5. In captives fat stores are typically 2–3 times greater at the onset of molt but disappear rapidly during the early weeks of molt, as they are probably mobilized for energy utilized in feather synthesis and associated energy cost of thermoregulation while the plumage is insulatively deficient. In captives the LI averaged about 5.4 (corresponding to an average of 1.4 g of fat) until the time when fat deposition is initiated. The level of fat reserves in captives appears to exceed by about 16% the level in feral birds (see King et al. 1965) whose LI in males and females during the first 3 weeks of molt averages 5.0 or less. Fat deposition occurs characteristically in late August in populations near Fairbanks. In this study and in one 10 years earlier (King et al. 1965), the onset of rapid body weight increase resulting from fat storage occurred on 25 August, at which time the molt is nearly complete.

Fat deposition occurs in captives in Pullman as well, but is less intense and subject to greater variation (see stage 5 in Table 5), which might be expected as the daylength and rate of photoperiod change at the latitudes of Pullman and Fairbanks differ markedly. Indoor birds maintained at a constant photoperiod showed either some or

TABLE 6
TOTAL BODY LIPID CONTENT (EXCLUSIVE OF PLUMAGE) AT DIFFERENT STAGES OF
POSTNUPTIAL MOLT IN CAPTIVE WHITE-CROWNED SPARROWS

Molt stage	N	Group CP ^a	N	Group CF ^a	N	Group E5 ^b	N	Group E15 ^b
0	3	2.25 ± 1.47 ^c (8.58 ± 4.88)	6	0.93 ± 0.23 (3.50 ± 0.69)	4	2.72 ± 1.27 (10.42 ± 4.54)	3	6.81 ± 0.66 (23.90 ± 3.43)
1	3	1.03 ± 0.32 (4.43 ± 1.31)	—	—	3	1.83 ± 1.02 (7.03 ± 3.40)	5	1.31 ± 0.22 (5.17 ± 1.02)
2	4	1.32 ± 0.18 (5.50 ± 0.83)	—	—	4	1.21 ± 0.26 (4.50 ± 0.77)	4	1.33 ± 0.19 (5.29 ± 0.76)
3	5	1.53 ± 0.25 (6.00 ± 0.88)	—	—	5	1.41 ± 0.25 (5.23 ± 1.05)	5	1.38 ± 0.17 (5.24 ± 0.44)
4	4	1.57 ± 0.44 (6.47 ± 1.74)	—	—	3	2.87 ± 1.40 (11.00 ± 4.73)	4	2.63 ± 1.51 (10.05 ± 4.86)
5	8	5.18 ± 1.50 (20.00 ± 4.86)	8	6.37 ± 0.96 (21.07 ± 2.35)	5	1.40 ± 0.50 (5.46 ± 1.86)	4	4.90 ± 2.92 (16.95 ± 8.64)

^a Caged outdoors. ^b Caged indoors. ^c Mean (g) ± standard deviation (percentage of whole wet weight in parentheses).

no late molt fattening. Group E5 birds showed no fattening at stage 5, but some birds in group E15 did fatten, as the LI varied in individuals from 7.8 to 25.6. The more probable explanation for this is that group E5 birds were placed indoors $\frac{3}{4}$ month earlier than were group E15 birds, the latter having the benefit of increasing summer daylength and suggesting that daily photoperiod increases greater than about 12 h may be necessary for the expression of late summer fattening. The doubling of body lipid seen between stages 3 and 4 in group E5 may have been a mere chance sampling of obese birds, because not all birds respond similarly with respect to fat deposition under artificial conditions of photostimulation.

Lipid reserves in other passerines during molt.—King et al. (1965) showed previously that body lipid is regulated at low levels in free-living Gambel Sparrows during the breeding season and is sustained throughout all but the last 1–2 weeks of molt in captives as well. In other passerines the lipid reserves may increase during the molt, an effect independent of photoperiodic stimulation resulting in hyperphagia and consequent obesity (King 1972). Fat stores in the Bullfinch are initially low (LI = 1.7–2.0) and by the end of molt have doubled, although the absolute weight of fat is still less than 1 g (Newton 1968).

The body weight of *Z. l. oriantha*, the montane race of the White-crowned Sparrow, is minimal before postnuptial molt, and increases throughout molt in both sexes owing to fat deposition (Morton and Welton 1973), but other unidentified components may have contributed to the increased weight. Fat deposition in *oriantha* accelerates in the last 10 days or so of molt as in *gambelii*, but the latter does not accumulate fat in substantial amounts during the molt except within a few days of its completion. The lipid index of the Chaffinch appears to parallel closely that of the Gambel Sparrow during the postnuptial molt. At the peak of molt, the LI is less than 4 (absolute weight of fat less than 1 g), but increases steadily near the end of molt to about 18 (Gavrilov and Dolnik 1974).

Energy reserves during molt.—From the few published studies of carcass composition during molt, it appears that fat stores are augmented to levels that are higher than those existing during the breeding period. In view of the diurnal variation of plumage-free lean dry weight that occurs in Bullfinches (Newton 1968), and the utilization of protein preferentially to fat in some waterfowl (Hansen 1962), or in

addition to fat in smaller birds (Ward 1969b), the level of fat reserves in molting birds is a misleading indicator of the physiological demands of molt. Birds that do not migrate may fulfill daily energy requirements during molt without daily augmentation of fat reserves other than that required for maintenance of nocturnal energy expenditure from thermoregulation. Low fat reserves may establish the lower limit during which a bird could survive an interval of forced fasting (inclement weather) or injury. Utilizing data from Ward (1969a) who found that structural lipid is about 1.32% of the body weight in the Yellow-vented Bulbul, I calculate that the Gambel Sparrow should have about 0.33 g of structural lipid as part of membrane phospholipids, for example.

In the lowest quantity of lipid found in a free-living White-crowned Sparrow (0.6771 g; body weight 23.5 g), the structural lipid should be about 0.31 g, leaving about 0.37 g as metabolizable fat. Assuming a mean daily temperature of 15°C and an existence metabolism of about 20 kcal/day during the first 2 weeks of molt, metabolizable fat could provide only about 17% of the daily energy budget, sufficient for about 4 h (physiological fuel value of lipid is 9.0 kcal/g). If reserves were closer to 0.93 g (group CF, stage 0), then this could provide 28% of the daily energy needs, or energy for about 6.5–7 h without feeding. Not included in these calculations are glycogen reserves, which may extend the period of nonfeeding for 1–2 h (Farner et al. 1961).

While it appears that stored energy reserves do not imperil the Gambel Sparrow at a time when feeding conditions extend for nearly 24 h daily, molting birds may be operating at times with marginal caloric reserves. Perhaps this is the reason why breeding and molting schedules in most passerines that molt fairly rapidly (50–70 days) do not overlap to any extent, if at all. The cumulative costs of feeding the young, of locomotion associated with feeding, and of feather synthesis and thermoregulation may overextend the energy-gathering capacity of the Gambel Sparrow. Any substantial overlap of breeding and molt cycles in this taxon could then be possible only by extending the molt period beyond the normal 60-day period. From this viewpoint, the rapid calendar molt may be acting as a selective pressure to separate temporally two potentially energetically costly events.

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