

### Carbon, Nitrogen, Ash, and Caloric Density of the Lean Dry Body Mass of White-crowned Sparrows During Postnuptial Molt

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Studies of postnuptial molt in the migratory White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) have revealed complex physiological and behavioral patterns that superficially include a reduction of lipid reserves (King et al. 1965), an increase in blood volume (Chilgren and deGraw 1977), and increases in total body water without attendant changes in the lean dry mass (LDM; Chilgren 1977; see also King 1980 for a summary of metabolic adjustments associated with molt). Preservation of the LDM in molting birds presupposes a level of nutritional adequacy or lipid stores to support plumage growth while maintaining normal body function. A behavioral component, depressed perch activity levels, is also observable in captive and free-living birds. While the function of this activity change is not clear, reduced activity may serve to minimize caloric expenditure or attract fewer predators to a passerine ill-equipped for rapid flight (Chilgren 1975).

Previous analysis of the body composition of this species during postnuptial molt has included lipid reserves, dry plumage weight, plumage water, body water, and the lean dry mass (Chilgren 1977). I subsequently analyzed the LDM for carbon, nitrogen, ash, and caloric density. Any structural or chemical modifications occurring within the relatively weight-stable LDM during molt in captives might then be identified by these techniques.

Two populations of birds were studied: those mist-netted in central and eastern Washington during the fall or spring migrations and a small group ( $n = 13$ ) of birds captured in late June at Fairbanks, Alaska (64°50'N) after the breeding season but before the molt. All Washington birds were eventually transferred to outdoor aviaries at Pullman, Washington (46°46'N) prior to the division of these birds into three groups of individually caged birds. Two groups were placed in constant conditions of light (LD 16:8) and temperature (5°C or 15°C), while the third was outdoors and shaded. All birds were provided with a chick-starter mash and water *ad libitum*. The small group of Fairbanks birds, which are difficult to obtain in large numbers at the breeding site before the molt, was inadequate for body composition study during molt and contributed to data either before (stage 1) or after (stage 5) molt. Hence, all data from birds during molt were derived from the three Pullman groups. Studies of the tempo and duration of post-

nuptial molt in birds at both locations are reported elsewhere (Chilgren 1978).

At each molt stage (see Table 1), a bird was sacrificed about 2 h after the end of its natural or artificial day. The digestive tract was air-flushed, and the entire animal was weighed to the nearest 0.01 g. De-feathered carcasses were lyophilized to constant weight (about 4 days). The gizzard contents of a desiccated carcass were removed, and carcass slices were prepared for fat extraction with diethyl ether for 24 h in a Soxhlet apparatus. These fat-free carcasses were subsequently oven-dried at 70°C to constant weight, ground in a Wiley mill (20-mesh screen), then further dried for 60 h at 50°C. Samples were taken for each of three procedures. Carbon and nitrogen determinations were made with a Hewlett-Packard 185B C-H-N analyzer, from which a computer-analyzed chromatogram provides critical information derived from a 20-s combustion cycle of prepared samples of 0.5–1.0 mg (weighed to  $10^{-3}$  mg). Ashing procedures involved igniting about 0.5-g samples to constant weight in a muffle furnace heated to 550°C, cooling the samples in a desiccator, and weighing them. Routine oxygen-bomb calorimetry with a Parr 1241 adiabatic calorimeter was performed with the third sample of 0.8–1.0 g. Ash, carbon, and nitrogen values were computed in g/kg dry weight, from which a percentage may be derived (e.g. 150 g/kg = 15%).

Elemental carbon levels tended to increase after molt onset in both indoor and outdoor Pullman groups, with large variations within groups (Table 2). Before the molt, carbon accounted for 42–44% of the LDM, increased to 40–47% during molt, and declined to 42–44% after molt. The magnitude of this increase is small but significant, especially in the 15°C group, when means were compared using a Student's *t*-test (Table 2). Postmolt carbon levels of the LDM

TABLE 1. Characteristics defining arbitrary stages of molt.

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

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TABLE 2. Elemental carbon composition in the lean dry mass of birds during various stages of postnuptial molt (mean g/kg  $\pm$  SD; *n* in parentheses).

Molt stage	Experimental group		
	5°C	15°C	Outdoors
0	423.5 $\pm$ 23.2 (4)	423.0 $\pm$ 12.2 (3)	437.3 $\pm$ 26.6 (3)
1	430.0 $\pm$ 23.8 (3)	496.5 $\pm$ 80.9 (6)	441.7 $\pm$ 30.0 (3)
2	435.6 $\pm$ 38.2 (5)	446.0 $\pm$ 11.5 (3)	465.7 $\pm$ 21.2 (3) <sup>b</sup>
3	445.8 $\pm$ 40.3 (5)	453.2 $\pm$ 8.4 (5) <sup>a</sup>	450.1 $\pm$ 75.5 (5)
4	493 (2)	462.5 $\pm$ 16.6 (4) <sup>a</sup>	423.5 $\pm$ 14.1 (4)
5	424.2 $\pm$ 29.7 (5)	445.1 $\pm$ 5.0 (4) <sup>a</sup>	429.6 $\pm$ 11.0 (5)

<sup>a</sup> Differs from stage 0 with  $P < 0.02$ .

<sup>b</sup> Differs from stage 5 with  $P < 0.05$ .

in the 15°C group were comparable to those of the Fairbanks group before ( $441.4 \pm 17.2$  g/kg,  $n = 5$ ) and after molt ( $446 \pm 19.1$  g/kg,  $n = 7$ ).

A similar pattern in LDM elemental nitrogen was not observed (Table 3). Nitrogen accounted for 12–14% (121–140 g/kg) of the LDM in all Pullman birds, and 14% (stage 1:  $136.8 \pm 5.0$  g/kg,  $n = 5$ ; stage 5:  $135.0 \pm 9.1$  g/kg,  $n = 7$ ) in the Fairbanks birds. An increase in LDM nitrogen occurred in the 15°C group at stage 1, with insignificant variation thereafter. Because of these nonconcordant patterns of elemental carbon and nitrogen composition during postnuptial molt, it appears unlikely that increased carbon represents a change in the protein content of the LDM. Because fat has already been extracted and the caloric density of the LDM is invariant (Table 4), the meaning of this compositional change in the LDM is currently unknown.

The carbon : nitrogen ratio (C:N) for the LDM was 3.2–3.4 before, about 3.5 during, and 3.4 after molt. The elevated ratio reflected the small increments in LDM carbon content noted above. An average C:N ratio for five animal and two plant proteins listed by Kleiber (1961: 43) was  $3.25 \pm 0.17$  (SD). This suggests that the LDM is predominantly protein since the LDM in these preparations includes only a small fraction of carbohydrate and a larger proportion of hydroxyapatite (bone minerals) that is nearly free of carbon

and nitrogen (Taylor et al. 1972). Because the carbon and nitrogen content in protein varies from 50 to 55% and from 13 to 19%, respectively (Oser 1965: 128), and because the C:N ratio is virtually unaffected, it is clear that the weight percentages of carbon and nitrogen in the LDM are decreased by the presence of nonprotein, neutral components that are relatively free of carbon and nitrogen. Under these conditions, the C:N ratio is a realistic estimator of the principal nature of the constituents within the lean dry body mass.

The LDM is about 15% inorganic material in molting and nonmolting birds (means ranged from 145 to 157 g ash/kg). At stage 0 of molt, the LDM ash content in all Pullman birds was  $151.2 \pm 6.1$  g/kg ( $n = 10$ ), similar to the Fairbanks group ( $152.0 \pm 4.7$  g/kg,  $n = 5$ ). These values were not significantly different after molt (stage 5). During molt, however, an insignificant (less than 7%) decline in LDM ash was observed, the lowest values appearing at stage 2 or 3 when the intensity of molt was greatest. Because this trend was observed in all three Pullman groups, it suggests that some mineral component is being expended during the molt. Were the dietary intake wanting in critical mineral nutrients, this trend in LDM ash might have been more apparent. Comparisons for other passerines indicate that the ash content in White-crowned Sparrows is about 3% greater

TABLE 3. Elemental nitrogen composition in the lean dry mass of birds during various stages of postnuptial molt (mean g/kg  $\pm$  SD; *n* in parentheses).

Molt stage	Experimental group		
	5°C	15°C	Outdoors
0	125.7 $\pm$ 5.9 (4)	123.0 $\pm$ 3.6 (3)	127.3 $\pm$ 11.8 (3)
1	125.0 $\pm$ 7.9 (3)	134.0 $\pm$ 12.4 (6)	127.7 $\pm$ 4.2 (3)
2	127.0 $\pm$ 11.7 (5)	138.7 $\pm$ 4.5 (3) <sup>a</sup>	130.3 $\pm$ 7.4 (3)
3	123.8 $\pm$ 7.8 (5)	137.2 $\pm$ 8.4 (5) <sup>a</sup>	126.8 $\pm$ 4.8 (5)
4	137.0 (2)	139.8 $\pm$ 4.3 (4) <sup>a</sup>	124.8 $\pm$ 5.2 (4)
5	121.4 $\pm$ 5.0 (5)	137.8 $\pm$ 2.7 (4) <sup>a</sup>	127.2 $\pm$ 4.6 (5)

<sup>a</sup> Differs from stage 0 with  $P < 0.05$ .

TABLE 4. Caloric values of the lean dry mass of birds at various stages of postnuptial molt (mean kcal/g  $\pm$  SD; *n* in parentheses).

Molt stage	Experimental group			
	5°C	15°C	P <sup>a</sup>	F <sup>b</sup>
0	4.35 $\pm$ 3.2 (4)	4.35 $\pm$ 8.9 (3)	4.27 (2)	4.27 $\pm$ 4.4 (3)
3	4.32 $\pm$ 3.4 (5)	4.40 $\pm$ 11.3 (4)	4.37 $\pm$ 4.6 (3)	—
5	4.34 $\pm$ 11.9 (5)	4.29 $\pm$ 4.7 (5)	4.33 $\pm$ 2.1 (3)	4.20 $\pm$ 9.8 (4)

<sup>a</sup> Outdoor group at Pullman, Washington.

<sup>b</sup> Outdoor group at Fairbanks, Alaska.

than in migrating Wood Thrushes (*Hylocichla mustelina*) and Kentucky Warblers (*Oporornis formosus*; Odum et al. 1965). The data for Alaskan White-crowned Sparrows (Chilgren 1977) now show that the ash content is 15.2% of the LDM (0.94 g) or 3.5% of the whole wet weight, a value that is nearly indistinguishable from other species (Olson and Ken-deigh 1980, Drobney 1982). This value (3.5%) agrees rather well with the skeletal mass of birds as predicted by the equation of Prange et al. (1979):  $Y = 0.065X^{1.071}$ , where *Y* is skeletal mass in kilograms and *X* is body mass in kilograms. A 25-g White-crowned Sparrow would contain 1.25 g of skeleton, or 5% of body mass. This value, however, presumably contains 30% organic material (Taylor et al. 1972), the remaining inorganic ash accounting for about 3.5% of body mass.

In a previous study (Chilgren 1977), the LDM contributed 22–23% of the body weight before and during molt. By subtraction, the ash-free LDM represents about 19% of the fresh weight of a bird not engaged in premigratory fattening. This percentage will necessarily decrease in this species immediately after the postnuptial molt prior to migration, as the lipid reserves increase from about 3% to more than 20% of the body weight (King and Farner 1965).

Caloric equivalents or heats of combustion ( $\Delta H$ ) of the LDM remained fixed near 18.00 kJ/g (4.3 kcal/g) at various molt stages (Table 4). The mean of 22 carcasses of the 15°C group, including 10 not reported in Table 4, was  $18.16 \pm 0.95$  kJ/g (coefficient of variation = 5), indicating the stability of this variable. The caloric equivalent or density of the LDM in captive White-crowned Sparrows is 8–10% less than in several species of migrating passerines (see Odum et al. 1965). The discrepancy is much greater (ca. 15%) with Mourning Doves (*Zenaidra macroura*, Brisbin 1968), but within 8% of Wood Ducks (*Aix sponsa*, Clay et al. 1979) and less than 6% in Japanese Quail (*Coturnix coturnix japonica*, Brisbin and Tally 1973). These variations in LDM caloric equivalents among species may reflect differences in fat extraction techniques, diet, or conditions of captivity, in which prohibition of flight influenced the LDM in some unknown manner.

Whether the LDM is "stable" as determined by these investigations is open to question. Composi-

tional changes in carbon and ash of less than 9% over the course of postnuptial molt may be significant if they actually reflect fluctuations in essential nutrients, including sulfur-containing compounds that are involved in supporting growth of new tissue. These gross determinations suggest only modest changes in the LDM. The relative stability of the LDM in weight as well as in carbon, nitrogen, and ash constituents is not surprising, given the *ad libitum* provisions of food and water with no opportunity for free flight. Experiments in which a monotonous diet and fluids are freely available preclude the option of food selection. The chick-starter mash used in these studies supports normal molt cycles but apparently is not a preferred food source when other diets are concurrently available (Murphy and King 1982). Whether different diets would result in fewer, if any, changes in the LDM is conjecture at this point. Nevertheless, the observed gross changes in the LDM variables studied indicate intriguing and subtle changes in body mass throughout the sequence of molt that are not clearly defined at this level of investigation.

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### Steller's Jays Steal Gray Jay Caches: Field and Laboratory Observations

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Steller's Jays (*Cyanocitta stelleri*) are nest robbers and have been observed to steal the food stores of other birds. Bent (1946) referred to them as "notorious nest robbers," and he suspected them of stealing the stores of the California Woodpecker (Acorn Woodpecker, *Melanerpes formicivorus*). Bailey (in Bent 1946) called them "robbers of the first order" and stated that they would "steal anything edible about camp." Steller's Jays have been observed to rob the seed caches of Clark's Nutcracker (*Nucifraga columbiana*, Tomback 1978). Although nutcrackers are vigilant for other nutcrackers and Steller's Jays before caching in seed storage areas, Tomback (1978) watched jays empty newly made caches just after nutcrackers left the cache sites. These observations suggest that food-cache pirating may be a frequent foraging behavior on the part of Steller's Jays.

We report here field observations of Steller's Jays pursuing Gray Jays (*Perisoreus canadensis*) and attempting to steal their caches. Gray Jays form boli of saliva-permeated food and store these in various places on conifers, such as on branch crotches, in bark crevices, and in foliage (Rutter 1969). The Gray Jays we observed, in turn, exhibited evasive behavior and in some cases avoided loss of caches. Because

these observations were made under relatively heavy snow conditions, these pirating behaviors could have been brought out by food scarcity. To test the effect of Steller's Jay presence on Gray Jay caching behavior, we conducted a short laboratory experiment. The results of these studies suggest that Gray Jay caching in the wild is regularly inhibited by the presence of Steller's Jays.

Field observations were made at Bear Lake (elevation 2,900 m), Rocky Mountain National Park, Colorado from mid-February to mid-March 1984. The forest in the vicinity of the lake consists primarily of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). We usually observed birds between 1000 and 1400, and attracted them to us by offering pieces of bread. Generally, Gray Jays, Steller's Jays, Clark's Nutcrackers, and Mountain Chickadees (*Parus gambeli*) came to feed. Most often, we fed only Gray Jays in order to collect data on their food-caching behavior. Gray Jays arrived in groups of 2-7, Steller's Jays in groups of 2-14, nutcrackers usually a short while later in groups of 2-6, and chickadees intermittently in groups of 3-7. The weather conditions were variable, with most days cloudy and cool (ca. 5°C). The snowpack for the months of February and March averaged 114.3 cm, which was about 42% higher than at the same time the previous year

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