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SULFUR AMINO ACID NUTRITION DURING MOLT IN THE WHITE-CROWNED SPARROW. 2. NITROGEN AND SULFUR BALANCE IN BIRDS FED GRADED LEVELS OF THE SULFUR-CONTAINING AMINO ACIDS

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ABSTRACT.—In an effort to estimate a critical concentration of dietary sulfur-containing amino acids (SAA) for molting birds, we measured nitrogen (N) and sulfur (S) balances before, during, and after postnuptial molt in five groups of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) fed isocaloric and isonitrogenous (17.4 kJ/g and 13.5% protein) diets in which SAA concentration ranged from 0.33 to 0.78%. These SAA concentrations approximate those found in natural diets and, as well, bracket the SAA requirements of poultry. Birds from all dietary groups showed positive N and S balances through six temporally equal stages of molt and in the nonmolting periods. Nitrogen retention differed significantly among molt stages but not among dietary groups. The grand average net N retention during molt (total N retention minus basal N retention) was 623 mg/25-g bird. Sulfur retention differed significantly among stages and among dietary groups. However, because group differences occurred both during molt and in nonmolt, the net S retention during molt (total S retention minus basal S retention) did not differ significantly among dietary groups. The grand average net S retention during molt was 85.4 mg/25-g bird. These results indicate that molting White-crowned Sparrows are typically able to meet the protein and SAA demands of molt through their food (the critical dietary SAA concentrations being less than those likely to be found in natural diets), thus precluding the need to deplete tissue proteins.

Avian molt is a type of growth characterized primarily by protein accretion in the form of feathers, and secondarily by the regeneration of other epidermal structures (Spearman 1966, Payne 1972, Chilgren 1975). Despite its morphological restriction, this integumental growth can entail a deposition of a protein mass approaching, or even exceeding, one-fourth of the protein content of a bird's body (Mitchell et al. 1931, Newton 1968, Myrcha and Pinowski 1970, Gavrilov and Dolnik 1974, Chilgren 1977, Carey et al. 1978). Moreover, the cyst(e)ine content of the plumage is disproportionately large compared to its content in the mixed proteins of other tissues or foods (Nitsan et al. 1981, Murphy and King 1982a; cf. F.A.O. 1970, Scott et al. 1982). These observations have, for decades, led avian biologists to question the ability of birds to fulfill the protein demands, or more specifically the sulfur amino acid (SAA) demands, of molt through daily food intake alone. The availability of dietary SAA has often been invoked as a potential explanation for observed changes in body composition, feeding habits, or even energetics during molt (e.g., Hanson 1962, Newton 1968, Gavrilov and Dolnik 1974, Brake et al. 1979), on the assumptions that (1) endogenous SAA reserves will be used if exogenous sources are inadequate, (2) birds may choose foods on the basis of SAA content, or (3) food intake may be increased above caloric needs to fulfill SAA requirements.

The results of the few empirical investigations that have been conducted on these subjects thus far are equivocal. Ackerson and Blish (1926) reported a disproportionate nitrogen-sparing effect of supplemental cystine in molting domestic fowl (*Gallus gallus* var. *domesticus*) that were fed otherwise N-free diets. Subsequent experiments (Ackerson et al. 1928) using a corn/casein diet and cystine supplements, however, failed to show a beneficial effect of these supplements on body weight, egg production, or the dynamics of molt in fowl. Similar investigations involving a laying ration and methionine supplementation also were ineffective in shortening the molting period or in increasing post-molt egg production in fowl (Taylor and Russell 1943). Likewise,

both negative (or at least large reductions: Holman et al. 1945) and positive sulfur balances (Lintzel et al. 1929) have been reported for molting hens. The reduction of S retention during molt is particularly enigmatic in view of the substantial deposition of cyst(e)ine-S in the plumage. Such a reduction could plausibly indicate that an amino acid other than cyst(e)ine or methionine was limiting during molt in these hens. Alternatively, it might reflect a loss of chondroitin sulfate from bone if a cylic osteoporosis is, in fact, a typical concomitant of molt (Meister 1951, Zhand 1954).

In an effort to estimate a critical level of dietary SAA concentration during molt we measured nitrogen (N) and sulfur (S) balances of molting White-crowned Sparrows that were fed diets differing in cysteine and methionine content. We also measured metabolized energy intake and molt dynamics in these birds, with results reported in detail elsewhere (Murphy and King 1984a, b).

MATERIALS AND METHODS

The White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) used in these experiments were housed and acclimated to the experimental diets (Table 1) as described by Murphy and King (1982b, 1984b). We made the diets isonitrogenous by adjusting glutamic acid concentrations. The diets were essentially isocaloric. The mean heat of combustion (±SE) of triplicate samples from each of the five diets ($n = 15$) was 17.40 ± 0.13 kJ/g dry weight. We measured food intake and the production of excreta by the experimental birds (four or five in each dietary group) through alternating three-day periods during the postnuptial molt and the pre- and postmolt periods. We dried samples of excreta and food in an oven at 65°C (Blem 1968), stored them in desiccators, and subsequently analyzed them for N content by the micro-Kjeldahl method (Horwitz 1980) and for S content by atomic emission spectrometry (Soils Analysis Laboratory, University of Idaho). To prepare samples for S analysis we combusted approximately 1 g of dried excreta in a bomb calorimeter, collected the methyl orange/H_2O washings, and brought them to a volume of 100 ml with 0.1 N HCl to minimize bacterial contamination. We also wet-ashed (nitric acid/perchloric acid: Horwitz 1980) samples of all diets and 10 randomly selected excreta samples in order to cross-check the reliability of S-analysis initiated by ashing by combustion. The average difference of S-concentration in samples prepared by these two methods was less than 5%. We measured the N and S content (duplicate and sometimes triplicate samples) of excreta from all birds and all three-day trials. We routinely verified the accuracy of the N analyses by measuring N concentrations in glucose (blank control), glutamic acid, cystine, and tyrosine.

TABLE 1. Composition of the experimental diets.[a]

Component	Diet A	B	C	D	E[c]
SAA[b]					
As % of diet	0.33	0.48	0.63	0.78	0.69
As % of protein	2.50	3.66	4.82	5.99	5.30
Cys as % protein	0.20	1.36	2.52	3.69	0.20
Met as % protein	2.30	2.30	2.30	2.30	5.10
Sulfur (μg/g dry wt.)[d]					
Calculated	1.70	2.10	2.50	2.90	2.50
Measured	1.73	2.18	2.52	3.00	2.67
Nitrogen (mg/g dry wt.)[d]					
Calculated	2.02	2.02	2.02	2.02	2.02
Measured	2.15	2.09	2.12	2.08	2.08

[a] Diets averaged 5.42% water and 13.5% protein by dry weight.
[b] Cyst(e)ine plus methionine.
[c] Molar concentration of total SAA in diet E equals that of diet C; cyst(e)ine concentration of diet E equals that of diet A.
[d] Calculated values are based on the composition of S- or N-containing components constituting the diets. Measured values are the means of triplicate measurements of S by atomic emission spectrometry and duplicate measurements of N by the micro-Kjeldahl method. See text for procedural details.

We calculated N retention as: (g food consumed × N content of food) − (g excreta × N content of excreta) and S retention by the same relationship of variables. We analyzed the results for the five diets and six temporally equal stages of molt and nonmolt (basal) primarily by a split-plot through-time ANOVA and Duncan's Multiple Range Test (Steel and Torrie 1960), and secondarily, as a cross-check, by one-way ANOVA of the areas beneath the curves of N or S retention vs. molt stage plotted for each bird individually.

RESULTS

NITROGEN BALANCE

We analyzed the mean gross nitrogen intakes (GNI) and mean gross nitrogen outputs (GNO) for six temporally equal stages of molt and in nonmolt (Fig. 1). Means that are not statistically different by Duncan's Multiple Range Test (alpha = 0.05) are bracketed. Because diet × stage interactions were significant for both GNI ($P = 0.0010$) and GNO ($P = 0.0022$) the main effects of diet and stage cannot be evaluated directly. Because the five diets were isonitrogenous, differences in GNI directly reflect differences in food intake. Food intake, in turn, reflects differences in the efficiency of energy utilization and the level of energy expenditure (Murphy and King 1984b). Differences of GNI among groups were compensated by differences in GNO, with the result that analysis (split-plot ANOVA) of total N retention (GNI − GNO, mg/day per 25-g bird) through molt

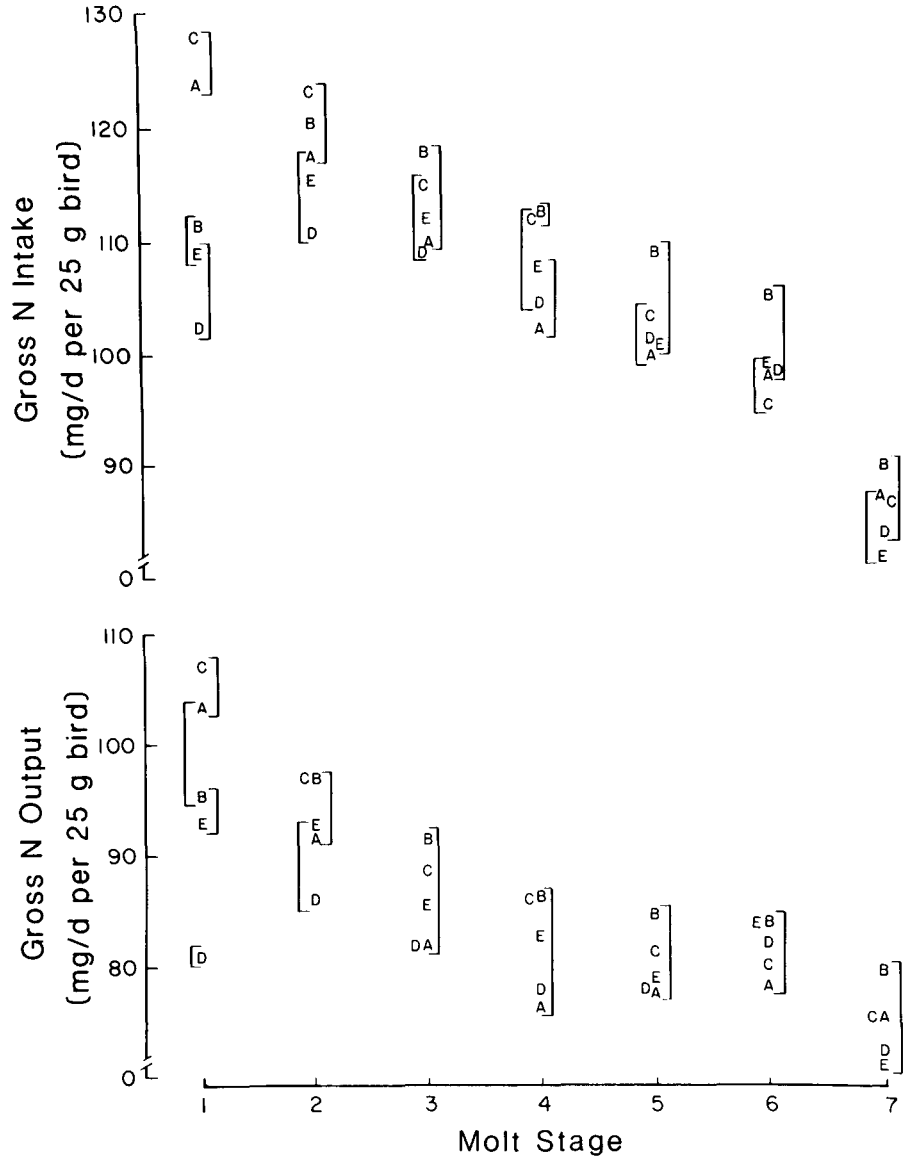

FIGURE 1. Components of nitrogen balance (means) in relation to diet and molt stage. Letters designate the means of the corresponding dietary groups. Means that do not differ significantly ($P > 0.05$) are bracketed.

and in nonmolt stages revealed no significant diet × stage interaction ($P = 0.526$) and no significant differences among diets ($P = 0.794$). Likewise, one-way ANOVA of the areas defined by curves of N retention for individual birds showed no significant differences in net N retention among the dietary groups (Table 2). Differences of N retention by all experimental birds among stages of molt, however, were highly significant ($P = 0.0001$, Fig. 2).

The basal nitrogen retention of nonmolting White-crowned Sparrows was statistically indistinguishable among the five diets (Duncan's Multiple Range Test, alpha = 0.05), and averaged (±SE) 10.94 ± 0.48 mg/day per 25-g bird, or 0.44 mg/g-day. This is virtually identical with the value reported by Parrish and Martin (1977) for adequately fed nonmolting Dark-eyed Juncos (*Junco hyemalis*), and establishes our baseline for estimates of net N retention. Theoretically, a "basal" N balance in an animal not engaged in production should be zero, but, as in our experiments and in those of Parrish and Martin (1977), is commonly found to be slightly positive (cf. Waterlow 1969). Presumably this results from unmeasured (other than cloacal) routes of N loss such as N deposition in skin, bill, and claw growth outside of molt and N lost in integumental glandular secretions. Although there is some evidence for the existence of "protein reserves" (Fisher 1967), the capacity of animals

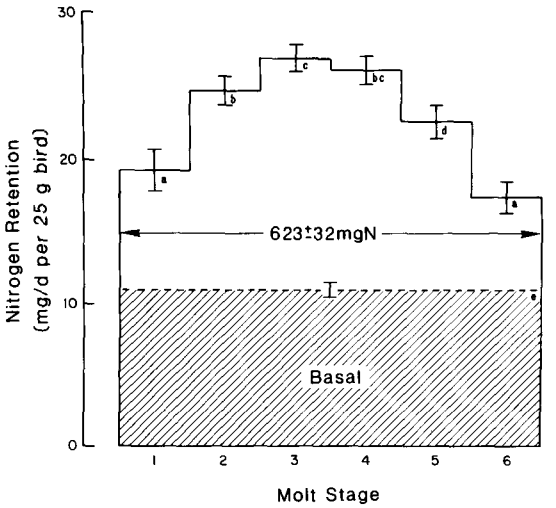

FIGURE 2. Mean (± SE) nitrogen retention through six stages of molt. Basal nitrogen retention is shown by cross-hatching. Stages having the same lower-case letters do not differ ($P > 0.05$). Net nitrogen retention (623 mg) equals the total area bounded by the histogram minus the basal area.

to accumulate protein solely as a nutritional buffer is undoubtedly limited, and probably accounts for little, if any, of the positive N-balance found in nonmolting White-crowned Sparrows and Dark-eyed Juncos.

Nitrogen retention increased progressively through stage 3 of molt and then declined through stage 6 to the basal nonmolt value (Fig. 2). This trend contrasts with GNI (and likewise with gross food intake), and conforms with our earlier interpretation (Murphy and King 1984b) that gross food intake during molt is regulated by energy requirements and that adequate SAA, and protein in general, is consequently supplied.

The *net* N retention (total N retention minus basal N retention) was strongly positive in all dietary groups, averaging (±SE) 623 ± 32 mg N per 25-g bird. Nitrogen deposition in the new plumage (1.65–1.85 g plumage × 15.22% N: Chilgren [1977] and Murphy and King [1982a], respectively) accounted for only 40% (251 mg) to 45% (281 mg) of the net N retained through molt. Some 342–372 mg of N must, therefore, have been either (1) retained in N-containing compounds other than the renewed plumage, or (2) lost from the body by routes that eluded our analytical methods. As a reasonable estimate, this amount of N is equivalent to 1.7–1.9 g of mixed protein retained or lost from the body, above the basal level and in addition to deposition in new plumage, during the molt (based on a conversion factor of 5.07 g of protein per g N in homogenized rat carcasses, including skin and fur [Buckley and Marquardt 1981]). Several routes of unmeasured N retention or loss could contribute to this quantity.

TABLE 2. Net nitrogen retention during molt in relation to diet.

Dietary group	Net N retention* (mg/25-g bird per molt) Mean	SE
A	660	90
B	646	56
C	642	61
D	602	47
E	554	121

* Net N retentions (as measured by areas beneath curves of N retention vs. time in individual birds) do not differ significantly ($P > 0.05$) by one-way ANOVA.

First, as is typical of small birds kept in cages and handled frequently, the White-crowned Sparrows in our experiments occasionally lost partly grown feathers. The tail is especially susceptible to this artifact of handling. Although we did not have the foresight, or necessarily the opportunity, to recover and weigh all partially grown feathers lost by the birds, our detailed records of their molt patterns nevertheless show that they typically grew as many as one to three partial tails before successfully replacing the rectrices. Our records also show that all birds grew at least an additional two-thirds of a tail. As the rectrices amount to about 7.5% of the total plumage mass (Murphy and King 1984a), this loss and regrowth inflates N retention in plumage by at least 15–20 mg.

Second, as mentioned in passing earlier, the postnuptial molt entails the regeneration of epidermal structures other than feathers. These include the corneus layer of the skin, the podotheca, the claws, and in some cases elements of the rhamphotheca (Payne 1972). We know that at least the stratum corneum and the podotheca are shed and replaced by White-crowned Sparrows during the postnuptial molt (Chilgren 1975; Murphy, pers. observ.). The renewal of these structures as well as the synthesis of the sheaths that temporarily encase every growing feather undoubtedly contribute to the positive N balance during molt, but we are unable to estimate reliably the quantities of N retained. This is a major challenge to analytical ingenuity in future investigations.

Third, additional routes of N sequestration might include the protein constituents of the feather pulp, the 53% increase of the erythrocyte count (Chilgren and de Graw 1977), the substantial expansion of plasma volume (W. de Graw and M. Kern, pers. comm.), and, in some species, a gain in total carcass protein during molt. Pulp, erythrocyte, and plasma proteins are potentially reusable, so their con-

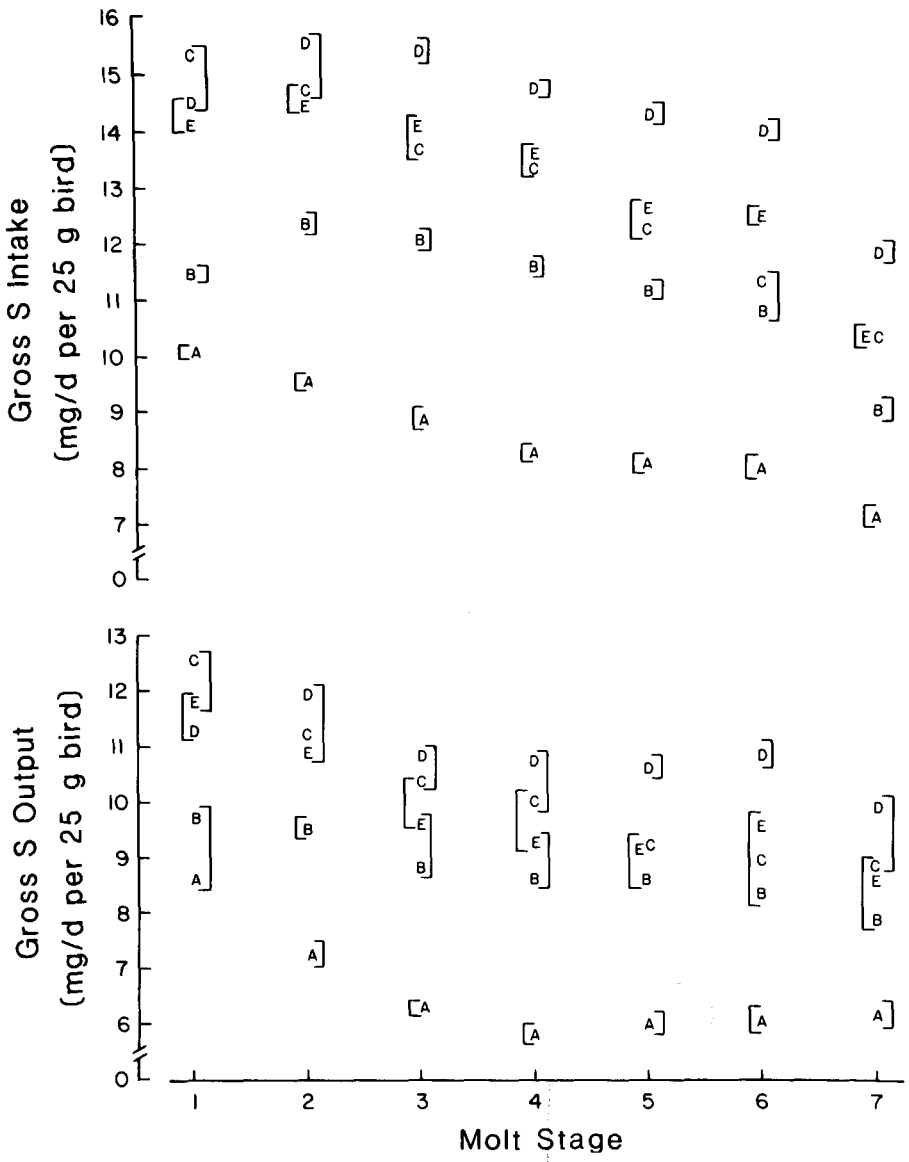

FIGURE 3. Components of sulfur balance (means) in relation to diet and molt stage. See Figure 1 for explanation of symbols.

tributions to a net N retention are impossible to estimate at present. Although a net gain of carcass protein during molt has been reported in Eurasian Bullfinches (*Pyrrhula pyrrhula*; Newton 1968), Snow Geese (*Chen caerulescens*; Ankney 1979), and in Brant (*Branta bernicla*; C. D. Ankney, pers. comm.), the data on this subject in the White-crowned Sparrow are equivocal (Chilgren 1977). It is also unlikely that a restoration of an earlier protein depletion explains part of the net N retention during molt in this species, as N-balance remains positive (equal to basal) even during the sharp reduction of body mass that occurs during the premolt and early-molt periods in this species (cf. Fig. 2 in this report and Fig. 3 in Murphy and King [1984b]).

Finally, even the most meticulous experimental methods in nutrient-balance studies apparently tend to err toward overestimating retention (Waterlow 1969). It is therefore important to be cautious in the interpretation of results. We suggest that such errors, if any, tend to be self-cancelling in comparative studies among dietary groups, which is the primary objective of this investigation. We are currently studying absolute changes in protein metabolism in molting birds that do not rely on N-balance techniques.

SULFUR BALANCE

White-crowned Sparrows in all dietary groups remained in positive sulfur balance throughout the molt, in accord with the results of Lint-

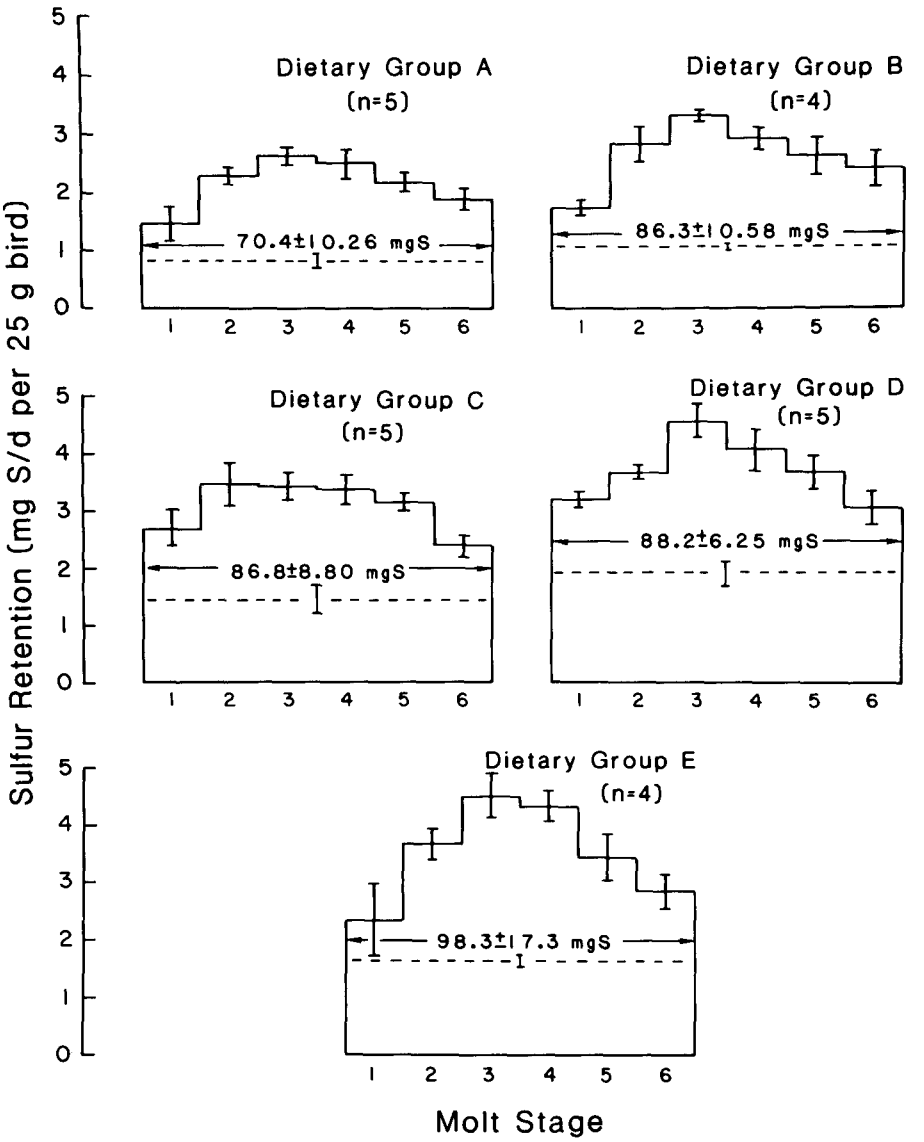

FIGURE 4. Mean (± SE) sulfur retention through six stages of molt. Basal sulfur retention equals the area beneath the broken horizontal line. Net sulfur retention equals the total area bounded by the histogram minus the basal area. See Table 3 and the text on the significance of dietary differences and stage differences.

zel et al. (1929) but at odds with those of Holman et al. (1945) in domestic fowl. The patterns of gross sulfur intake (GSI) and gross sulfur output (GSO) are shown in Figure 3. As before, the letters designate the means for the corresponding dietary groups and the brackets exclude significantly different means (Duncan's Multiple Range Test, alpha = 0.05). Both GSI and GSO showed significant interactions between diet and stage (split-plot through-time ANOVA, $P = 0.0001$ and 0.0137, respectively). These interactions appear to be explained best by a tendency of the birds to regulate food intake according to energy demands, so that changes in the efficiency of energy utilization and in energy expenditure influence food intake, and thereby the intake of dietary constituents (Murphy and King 1984b). Sulfur consumption and excretion through molt (stages 1–6) and in the postmolt period (stage 7) almost invariably reflected the sulfur concentrations of the experimental diets (except for the interactions noted above).

Sulfur retention, like N retention, showed no significant diet × stage interaction ($P = 0.250$), and S retention differed among both diets and stages of molt ($P = 0.0002$ and 0.0001, respectively). Sulfur retentions through molt are plotted in Figure 4 for each of the five diets. Analysis of the main effects of diet and stage (Table 3) reveals that the *total* average S retention through six stages of molt and in the postmolt period (stage 7) differed significantly among the five groups and that S retention was

TABLE 3. Diet and stage differences (main effects of split-plot ANOVA) in gross sulfur retention in relation to diet and stage of molt.[1]

Category	Mean[2] (mg/25-g bird)
Dietary group	
A	1.99[a]
B	2.45[ab]
C	2.87[bc]
D	3.47[d]
E	3.27[cd]
Stage of molt	
1	2.32[a]
2	3.20[bc]
3	3.69[d]
4	3.44[cd]
5	3.02[b]
6	2.53[a]
7	1.40[e]

[1] Diets or stages with different superscripts differ significantly ($P < 0.05$). Values for individual groups by stage are shown in Figure 4.
[2] Means for dietary groups are means of *all* seven stages. Means for stages are means of *all* dietary groups.

a positive function of S concentration in the diets. However, because these differences were reflected in both molt and postmolt (basal) stages, the *net* S retention during molt, as computed from the individual S-retention curves of the 23 birds in this experiment, did not differ significantly among birds when tested by one-way ANOVA ($P > 0.05$). Group A, however, was notably lower than the others. Molt-stage differences in S retention in relation to diet were similar to those already reported for N retention (cf. Figs. 2 and 4).

The grand average (±SE) net sulfur retention during molt for all dietary groups combined was 85.44 ± 4.708 mg S/25-g bird per molt. The S concentration of the plumage of the White-crowned Sparrow averages 3.14 ± 0.057% (Murphy and King 1982a) and accounts for 51.8–58.1 mg of the net S retention during molt (1.65–1.85 g of plumage × 3.14% S). Net S retention in excess of this presumably was involved in the synthetic processes previously discussed in connection with net N retention. It is not apparent why the basal S retention was so large, or why the S retention was additive to the basal retention during molt in birds consuming the diets with the larger S concentrations. In view of the lack of significantly larger N retention by the birds in these same groups it does not seem likely that the extra S that they retained contributed to protein synthesis. Even in mixed proteins in which the SAA concentration is as large as in feather keratins, the N:S ratio is of the order of 4.8:1. For each additional mg of S (atomic wt. = 32.064) retained, 2.1 mg of N (atomic wt. = 14.0067) would be retained. If the ratio were estimated on the basis of plumage-free carcass composition, in which the SAA are less concentrated, it would be even larger. That the total (gross) S retention differed significantly among diets, while total (gross) N retention did not, suggests that much of the additional S retained by the high dietary S groups was probably in inorganic compounds. The retention of this S in either organic or inorganic form is enigmatic and merits further investigation. Reports of the occurrence of a cyclic osteoporosis during molt (Meister 1951, Zhand 1954), presumably involving a loss and replacement of chondroitin sulfate, and of a preferential uptake of radioactive sulfates by the gizzard (Machlin et al. 1954) suggest that the skeleton and the gizzard merit special attention in this regard.

DISCUSSION AND CONCLUSIONS

The foregoing data support the conclusion reached by Newton (1968) and Ankney (1979) that molting birds are typically able to meet the protein (specifically, the SAA) requirements of feather synthesis through their food, thus sparing other vital body proteins from depletion. The range of SAA concentrations used in our experiments bracket those found in natural foods as well as the SAA requirements of poultry (Murphy and King 1984b). The availability of SAA from these diets is probably somewhat better than in natural foods, since about 25% of the SAA were in crystalline form (75% in intact casein). Nevertheless, even in view of this experimental artifact, an SAA concentration of 0.33% and a cyst(e)ine concentration amounting to 0.2% of dietary protein (about 0.03% of the diet) would be difficult if not impossible to find in the mixed proteins of natural diets. The birds consuming these ostensibly minimal SAA concentrations molted normally and showed a strongly positive N balance (indistinguishable from that of birds consuming diets in which SAA concentration was as high as 0.78%). This suggests that it would be timely to reevaluate current views of the dynamics of protein and amino acid nutrition in molting birds. Although avian molt entails deposition of a protein mass that equals or even exceeds one-quarter of the total protein content of a bird, the process of feather replacement is relatively slow. The molt spanned 54 days in the birds in our experiments, and other passerines typically take longer than this. The *daily* nutrient demands of feather synthesis should be evaluated in relation to the concurrent maintenance demands and the *sum* of both demands evaluated in relation to dietary intake. At peak molt (stage 3), the birds in our experiments retained about

27 mg N/day per 25-g bird, and from 2.7 (group A) to 4.6 (group D) mg S/day per 25-g bird. The average N intake in stage 3 was 113 mg/day per 25-g bird, and the average S intake ranged from 8.9 to 15.4 mg/day per 25-g bird in groups A and D, respectively. Thus, less than 25% of the ingested N (in these diets, virtually all of it as protein N) was diverted to the synthesis of N-containing compounds, the remainder being either unabsorbed and lost in feces or excreted in urine. Likewise, only 38% of ingested S was retained.

Similar estimations using the nitrogen and sulfur contents of raw diets yield similar results. The average White-crowned Sparrow at mid-molt metabolizes about 74 kJ/day in captivity (Murphy and King 1984b). On a diet of plant seeds containing 16.75 kJ/g (80% utilizable) and 15% protein (values after Kendeigh et al. 1977), about 5.5 g of seeds would be necessary to satisfy energy requirements. This quantity of seeds would provide about 825 mg of protein. At mid-molt, White-crowned Sparrows retain about 27 mg of N per day, or about 169 mg of protein per day (N × 6.25, the average N conversion factor). Thus, nearly 80% of the ingested protein either is oxidized completely or is converted to nonprotein compounds (e.g., fat or carbohydrate). Even if 300–400 mg of tissue protein were deposited by day and catabolized by night (Gavrilov and Dolnik 1974, Newton 1968), 31–43% of the ingested protein would be used for purposes other than protein synthesis.

Let us assume, as did Kendeigh et al. (1977), that cyst(e)ine constitutes about 1.5% of seed protein, and also that at least as much methionine is present (based on our estimates from the F.A.O. [1970]). We can then calculate from the dehydrated molecular weights of cys and met that the minimum sulfur concentration in seeds (exclusive of nonprotein S) is about 1.26 mg/seed, or 6.9 mg/5.5 g of seed. Sulfur retention at peak molt in our group A averaged 2.7 mg/day per 25-g bird, or 39% of the minimal estimate of S intake per day by a White-crowned Sparrow if it were consuming a diet of seeds. In group D, S retention averaged 4.6 mg/day per 25-g bird, or 67% of the estimated minimal intake. Recall, however, that the additional S retention by birds consuming the higher dietary SAA concentrations did not confer on them any detectable advantage in plumage regeneration (Murphy and King 1984a) or in N retention.

The foregoing estimates as well as the results of our measurements of nitrogen and sulfur balance during molt indicate that attempts to assess the protein (SAA) demands of feather synthesis and the dietary stresses of molt by comparing the amino acid compositions of food and feathers (Gavrilov and Dolnik 1974, Kendeigh et al. 1977) are unrealistic. The concurrent demands for amino acids in the synthesis of body proteins and the equivalent replacement of endogenous N loss also influence the spectrum of amino acids required by molting birds. Consequently, the fact that the mixed proteins of nonfeather tissues contain a much lower SAA concentration than feathers dilutes estimates of SAA requirements based simply on food/feather comparisons. In fact, if the nocturnal catabolism and diurnal replacement of protein accelerate during molt, as described by Gavrilov and Dolnik (1974) and Newton (1968), then the influence of the relatively high cyst(e)ine concentration in keratins on the daily profile of amino acid requirements will be slight. These considerations begin to explain how and why molting birds do, in fact, succeed in nature and are much less susceptible to nutritional constraints than has been imagined.

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