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SULFUR AMINO ACID NUTRITION DURING MOLT IN THE WHITE-CROWNED SPARROW. 1. DOES DIETARY SULFUR AMINO ACID CONCENTRATION AFFECT THE ENERGETICS OF MOLT AS ASSAYED BY METABOLIZED ENERGY?

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ABSTRACT.—To test the hypothesis that the dietary intake of the sulfur-containing amino acids (SAA) methionine and cyst(e)ine affects energy intake or the allocation of energy to production and oxidation, respectively, we fed five groups of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) five isocaloric, isonitrogenous diets before, during, and after their postnuptial molt. The diets ranged in SAA content from sub- to superadequate in relation to standards established for poultry, and from very low to very high in relation to the SAA content of natural foods. The patterns of plumage replacement were indistinguishable among the five groups. The body weights of all birds decreased sharply at the onset of molt, as is typical for this and other species, and then gradually increased through early molt and stabilized during mid- and late molt. The components of energy balance (gross energy intake, energy utilization coefficient, caloric density of excreta, total excretory energy output) did not differ significantly or consistently among the five groups. Likewise, the net energy of molt, as estimated by subtracting the maintenance requirement for metabolized energy from the expenditure during molt by the same birds, ranged from 582 to 611 kJ, but without significant differences among the groups and without consistent correlations to the diets. The grand average was 605 kJ/25-g bird. Hence, we are unable to verify the predictions of the amino acid model for the determination of the energy requirements of molt.

In a review of the energetics of avian molt, King (1981) estimated that the mean (±SEM) energetic cost of molt in a small passerine is 469 ± 34 kJ/g of plumage replaced. Dividing the heat of combustion of feathers (22 kJ/g dry weight: Murphy and King 1982a) by this estimate yields an energetic efficiency for feather synthesis of only 4.7%. Such a low efficiency contrasts sharply with the estimated 40–60% efficiency in the utilization of metabolizable energy for energy deposited as tissue protein by growing homeotherms, and with the 30–88% efficiency for energy deposited as egg protein (Van Es 1980). This suggests either that King's estimate is erroneous or that energy-demanding processes in addition to keratin synthesis are characteristic of molt but are either more intense than in other conditions of protein synthesis or do not occur in such conditions.

Gavrilov and Dolnik (1974) postulated that the apparent discrepancy between the energy cost of molt and the energy deposited in plumage might be accounted for by the energy-demanding conversion (oxidation) of large amounts of food to extract the indispensable amino acids cysteine or cystine (henceforth cyst(e)ine) necessary for feather synthesis. This hypothesis, which we will call the "aminostatic hypothesis of molt energetics" (or simply the "aminostatic hypothesis") because it depends on an aminostatic regulation of food intake, is described by the equation (Kendeigh et al. 1977):

$$NEM = [W_{pl} \times A_{pl}] \cdot [(GEI \times MEC)/(A_{pr} \times Pr)]$$

where NEM = the net energy cost of molt (kJ), W_{pl} = the weight of new plumage (g), A_{pl} = the cyst(e)ine concentration in feathers (g/g), GEI = the heat of combustion of food (kJ/g), MEC = the metabolizable energy coefficient (%), A_{pr} = the cyst(e)ine concentration in dietary protein (g/g), and Pr = total protein content of the food (g/g). In seven studies of various subspecies and age classes of House Sparrows (*Passer domesticus*) and Common Chaffinches (*Fringilla coelebs*), the estimates of the energetic cost of molt calculated according to this equation agreed within 0.5%

with those measured by energy balance methods (Gavrilov 1974). Through this "aminostatic" equation, Kendeigh et al. (1977) calculated that nearly a 50% reduction in the net energy cost of molt would result from a shift from granivorous to insectivorous feeding by molting birds.

A critical evaluation of the assumptions implicit in the "aminostatic hypothesis" (King 1981, and the following text) led us to question whether (1) the narrow range of cyst(e)ine concentration (A_{pr} = 1.2–1.5%) in the experimental diets used by Gavrilov (1974), or (2) the potential for error in his estimates of several variables in the aminostatic equation, had not resulted in a remarkable concordance between direct and indirect measurements.

In the first place, the "aminostatic hypothesis" requires that feeding be regulated by the availability of the limiting amino acid (presumably cyst(e)ine during molt) so that food consumption will *increase* to a level that satisfies metabolic demands for amino acids. On the contrary, however, existing evidence for a partial role of aminostatic control of feeding (Leung and Rogers 1969, 1971; Robinson 1974; Montgomery et al. 1978; but see also Kennedy 1953, Le Magnen et al. 1973, Epstein et al. 1975, Ritter et al. 1978) indicates that food intake is *depressed* by amino acid imbalances or deficiencies. Numerous studies of SAA requirements in both domestic fowl (*Gallus gallus* var. *domesticus*) (e.g., Leveille et al. 1961, Khalil et al. 1968, Graber and Baker 1971, Boomgaardt and Baker 1973, Potter and Shelton 1979) and laboratory rats (e.g., Seligson and Rotruck 1983) as well as studies of other essential amino acids (e.g., Fisher et al. 1960, Sugahara et al. 1969, Scott et al. 1982) have reported decreases, not increases, of food intake when dietary amino acid concentrations are inadequate. This seems to suggest that if aminostatic regulation acts at all in *daily* feeding behavior in response to mixed diets it is more likely to affect the choice of foods rather than the total amount (in kJ) eaten. Regardless of the mechanism (aminostatic, glucostatic, lipostatic) that controls food intake, the available evidence makes it unlikely that food consumption will substantially increase for an extended period to supply a limiting amino acid.

In the second place, even if molting birds can consume more than enough energy and other nutrients in compliance with the "aminostatic hypothesis," the reliable use of the aminostatic equation requires that the diet consumed by birds before the onset of molt *exactly* meets the cyst(e)ine requirement (or, more correctly, SAA requirement: see beyond). This would mean that the SAA requirement during molt is entirely additive (i.e., before molt the diet cannot contain excesses of SAA that may be shunted from oxidative pathways to keratin synthesis at the onset of molt).

In the third place, the aminostatic equation neglects the potential role of endogenous SAA reserves (e.g., tissue proteins or glutathione) and assumes that all SAA for keratin synthesis is obtained from the diet. Reports of increased glutathione (or at least free sulfhydryl) concentration in the blood of domestic fowl during molt (Goto and Okamoto 1965), however, make this assumption questionable. Glutathione is a tripeptide (glu-cys-gly) that has been shown to serve as a cyst(e)ine reservoir also in laboratory rats during periods of dietary SAA deficiency (Tateishi et al. 1977, Cho et al. 1981, Seligson and Rotruck 1983). Additional evidence of the occurrence of endogenous SAA reserves during production comes from studies of egg-laying domestic fowl (Leveille et al. 1961). Hens that were fed too little methionine promptly ate less and soon after stopped layings eggs. Food consumption then increased to control levels, and after a few days egg-laying resumed and food consumption decreased sharply. Egg-laying resembles molt in that a largely proteinaceous product is synthesized and then excreted from the metabolic pool. The results of Leveille et al. (1961) suggest that the SAA requirements of egg-laying hens exceeded SAA availability from the diet, which depressed food intake and inhibited egg-laying. The diet, however, met and apparently exceeded the maintenance requirements, so that normal food consumption was restored when egg-laying ceased and tissue proteins could likewise be restored. The response of hens to SAA deficiency during egg production thus sharply contrasts with the predictions of the "aminostatic hypothesis" of molt energetics.

In the fourth place, the aminostatic equation omits a coefficient of utilization for dietary SAA, apparently assuming that 100% of dietary cyst(e)ine is absorbed and incorporated into protein. In reality, cyst(e)ine availability from dietary protein may range from almost negligible, as in the case of keratins (Scott et al. 1982) to nearly complete in other kinds of proteins (Baker 1976). Moreover, the apparent availability of SAA (methionine plus cyst(e)ine) for tissue growth and feathering in male domestic fowl averages only 68% of the animal's *requirement* (Scott et al. 1982). This occurs because the SAA are involved in metabolic functions apart from their role as substrate for protein synthesis (e.g., cyst(e)ine as a sulfate donor, and methionine as a methyl donor and

TABLE 1. Sulfur amino acid concentrations in the experimental diets.[a]

Diet	TSAA[b] (% diet)	Cyst(e)ine (% protein)	Methionine (% protein)
A	0.33	0.20	2.30
B	0.48	1.36	2.30
C	0.63	2.52	2.30
D	0.78	3.69	2.30
E[c]	0.69	0.20	5.10

[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.

precursor of cyst(e)ine). In short, even if an SAA-containing protein is completely digested and absorbed, it is unlikely that all of the SAA entering the metabolic pool will be used in protein synthesis.

Finally, and perhaps most importantly, the aminostatic equation's exclusion of dietary methionine concentration from the calculation of the net energy cost of molt ignores the metabolic conversion of methionine to cyst(e)ine. Studies of both laboratory rats (Sowers et al. 1972) and domestic fowl (Graber and Baker 1971) have shown that the molar efficiency of this conversion closely approaches 100%. Furthermore, the entire SAA requirement (methionine plus cyst(e)ine) can be met by adequate amounts of dietary methionine alone.

In sum, most of the implicit assumptions of the "aminostatic hypothesis" of molt energetics appear to be questionable when examined in relation to the results of investigations of domestic animals. Nevertheless, there is some tenuous evidence that food intake and energy expenditure increase in growing domestic fowl when they are fed inadequate SAA concentrations (Baldini 1961, Shoji et al. 1966, Solberg et al. 1971; cf. Carew and Hill 1961, Davidson et al. 1964). This, plus the remarkable concordance between measured and predicted *NEM* reported by Gavrilov (1974), prompted us to investigate energy utilization by molting White-crowned Sparrows when fed graded levels of SAA. In effect, this is an empirical test of the "aminostatic hypothesis" of molt energetics.

MATERIALS AND METHODS

We captured White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) during their spring migration through eastern Washington and kept them in an outdoor aviary where chick-starter mash and water were freely available. About one month before molt began we transferred the experimental birds from the outdoor aviary to individual cages (22 × 40 × 27 cm) in constant-condition rooms (21°C, LD 16:8). For 12 days we fed these birds (four to five per group) the basal synthetic diet described by Murphy and King (1982b), and then transferred them to five different experimental diets identical in composition to the basal diet except for graded SAA concentrations (Table 1). We made the five diets isonitrogenous (13.5% protein = 2.12% nitrogen × 6.38 [the Kjeldahl conversion factor for casein]) by adjustments of glutamic acid concentration. Differences in the caloric density of the five diets were trivial, and the grand average of 15 measurements (three each of five diets) of the heat of combustion at constant volume was 17.40 ± 0.13 kJ/g.

The experimental birds remained on their respective diets throughout the 90-day duration of the trials. We measured body weights and the status of molt (Murphy and King 1984a) every third day, and food intake and the production of excreta simultaneously throughout molt for three successive days alternating with three-day intervals. We later measured the caloric density of the excreta collections from all trial periods by oxygen-bomb calorimetry.

We analyzed the primary data by a split-plot through-time ANOVA and Duncan's Multiple Range Test (Steel and Torrie 1960), and examined the net energy cost of molt (the areas beneath plots of metabolized energy intake vs. days of molt for individual birds) for the dietary groups by one-way ANOVA. We cite the levels of statistical significance as the probabilities (P) that either sets of means are homogeneous or paired means are alike.

RESULTS AND DISCUSSION

The pattern of postnuptial molt in experimental groups of White-crowned Sparrows and the weight of plumage replaced are indistinguishable through a range of dietary SAA concentrations exceeding that of the present experiments (Murphy and King 1984a), which shows that the intensity of production in molt is alike among dietary groups. It remains to be shown from the results reported herein whether this uniformity is achieved by similar or dissimilar patterns of energy intake, excretion, and retention among the five dietary groups.

Figures 1 and 2 illustrate the relationships among the five groups in food intake (g/d, dry weight), energy utilization coefficient (UC, % of ingested energy not excreted in droppings), caloric density of excreta (kJ/g, dry weight), weight of excreta (g/d, dry weight), and excretory energy (kJ/d) through six temporally equal stages of molt and in nonmolt (stage 7). Gross food intake ($P = 0.0001$), the weight of excreta ($P = 0.0001$), and excretory

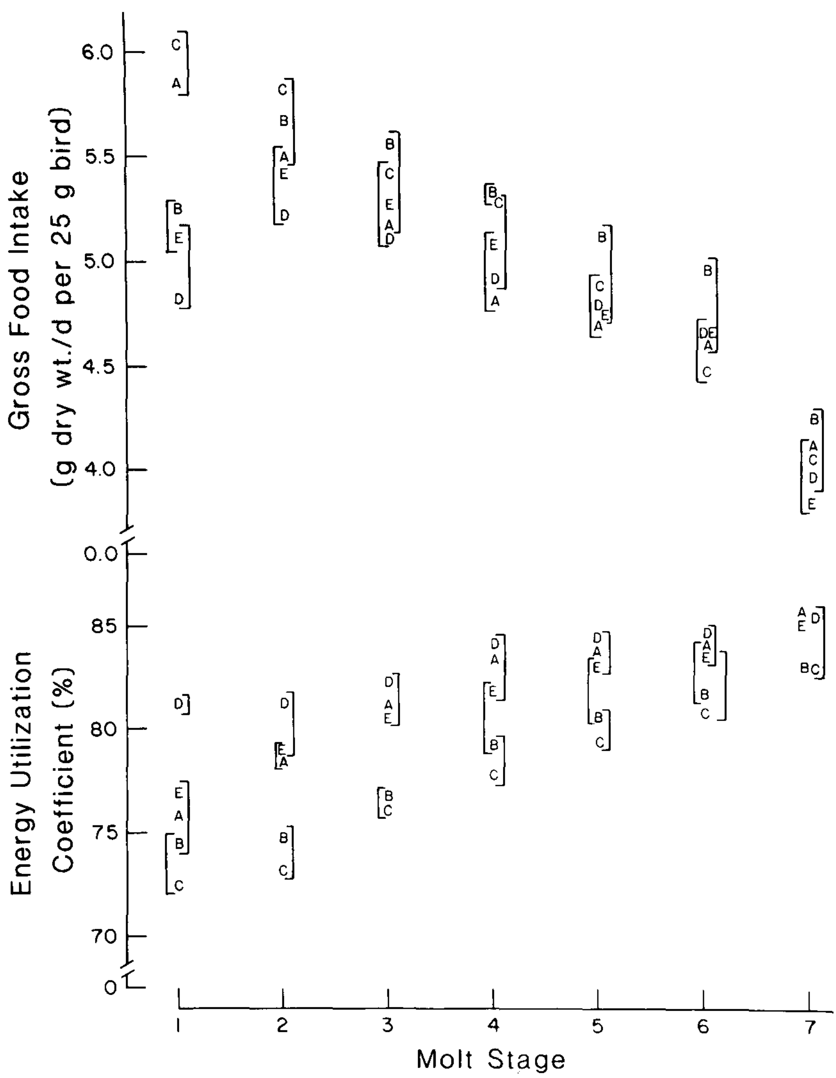

FIGURE 1. Food intake and energy utilization coefficient in relation to diet and molt stage. Letters designate the means of corresponding dietary groups. Means that are not significantly different ($P > 0.05$) are bracketed. Stages 1–6 are temporally equal (nine-day) stages of molt, and stage 7 is non-molt.

energy ($P = 0.05$) all showed significant diet × stage interactions, so that the main effects of diet and stage could not be interpreted separately. Nevertheless, the results of Duncan's Multiple Range Test (alpha = 0.05: Figs. 1, 2) did not indicate that the differences occurring among the 35 means (five diets and seven stages) in any of these variables were related to dietary SAA concentration. For instance, in the case of gross food intake this is best illustrated by comparisons of diet A (the lowest SAA and cyst(e)ine diet) with the other four groups. According to the "aminostatic hypothesis" the birds in group A should have consumed the greatest amount of food (Table 2); but, on the contrary, in seven stages of molt these birds never ate the maximum hypothetical amount of food predicted for either cyst(e)ine or SAA dietary concentrations at either 100% or 68% utilization. In two stages (4 and 5) they consumed the least amount of food of any of the groups (Fig. 1), although not significantly so in all comparisons. This precludes the operation of a mechanism that suppresses food intake in response to SAA inadequacy. Furthermore, with the exception of stage 1 (see beyond) food consumption did not differ significantly between birds consuming diet A (lowest in SAA and cys) and diet D (highest). That group C consumed significantly more food than groups B and E during stage 1 refutes any argument for an effect of diet on food consumption during this stage. Both SAA and cys concentrations of diet C exceeded those of diet B, while the SAA concentrations of diets C and E were equal, and the cys concentration

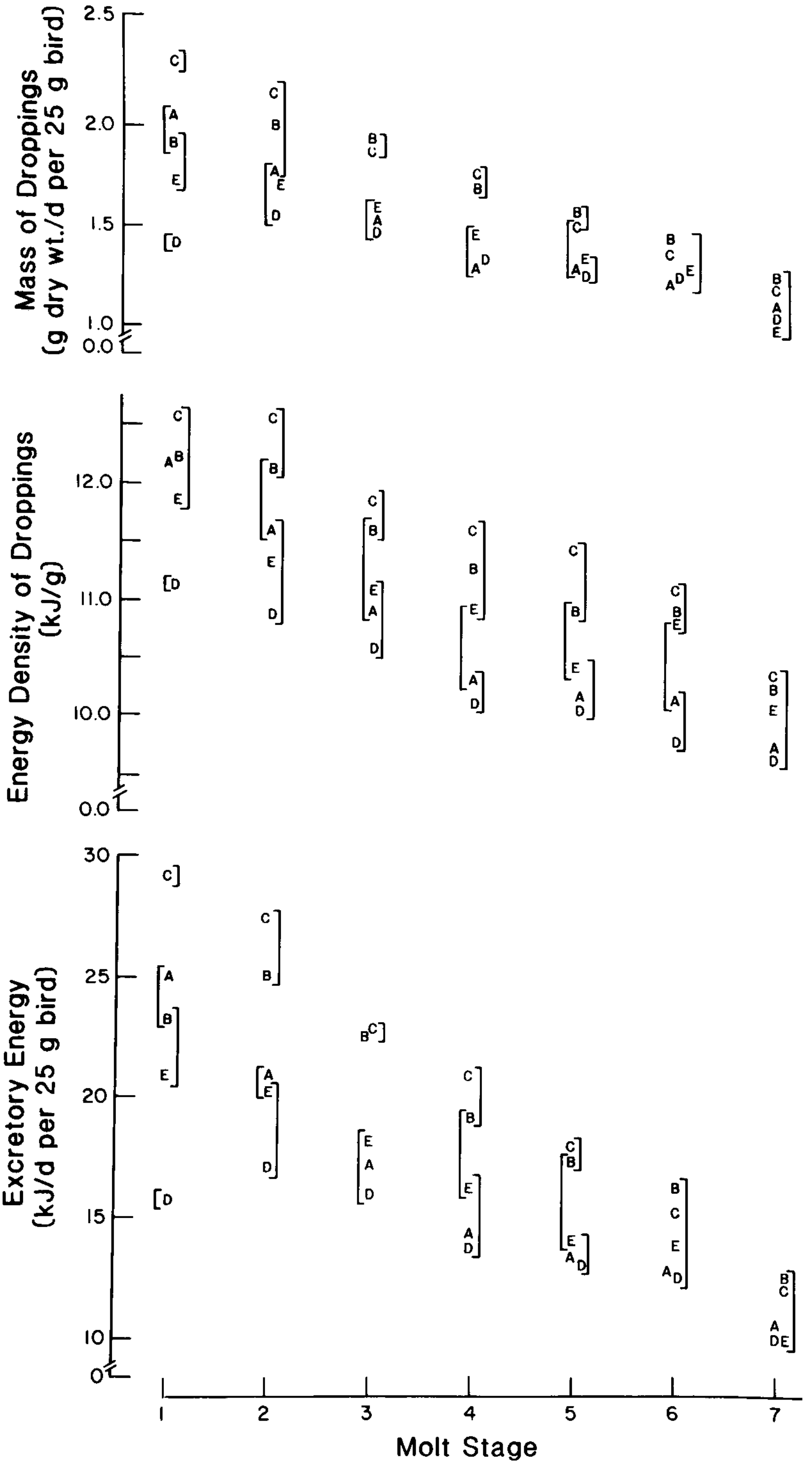

FIGURE 2. Excretory energy and its components in relation to diet and molt stage. See Figure 1 for explanation of symbols.

of diet C exceeded that of diet E. The total increase of food intake above the basal level during molt is given for each dietary group in Table 2. The agreement among groups in measured increases of intake is inconsistent with the predictions of the aminostatic equation. In fact, the measured food intake by group A was less than even that predicted for 100% utilization of methionine plus cyst(e)ine (total SAA). This implies either that in at least this

TABLE 2. Predicted (aminostatic equation) and measured increases of food intake above basal level during molt in relation to diet.

	Increase of food intake (g)				
	Predicted[a]				
	Cys utilization		TSAA utilization		
Diet	100%	68%	100%	68%	Measured[b]
A	590	868	57	84	43
B	87	128	37	54	43
C	47	69	27	40	44
D	32	47	21	31	42
E	590	868	27	40	45

[a] The quantity of food containing an amount of cyst(e)ine or TSAA (cyst(e)ine plus methionine) equivalent to cyst(e)ine contained in the new plumage, calculated according to 100% and 68% SAA availability (see Introduction). For use in TSAA predictions, moles of dietary methionine were converted to mg of available cyst(e)ine.

[b] The quantity of food necessary to supply the added energy expenditure of molt (Table 4), based on the average utilization coefficient through molt for the respective dietary groups (Table 3).

TABLE 3. Mean energy utilization coefficients (UC) in relation to diet and stage of molt.[1]

Category	UC, %
Diet	
A	81.8^{ab}
B	78.7^{bc}
C	77.5^{c}
D	83.4^{a}
E	81.4^{ab}
Stage	
1	76.2^{a}
2	77.4^{b}
3	79.6^{c}
4	81.3^{d}
5	82.3^{de}
6	83.0^{e}
7	84.5^{f}

[1] Means with different superscripts differ ($P < 0.05$) by Duncan's Multiple Range Test. The probability of homogeneity among means (by split-plot through-time ANOVA) is 0.065 for diets and 0.0001 for molt stages.

group endogenous reserves of SAA contributed to feather synthesis or, more likely (cf. Murphy and King 1984b), that the SAA in food needed to meet maintenance energy requirements exceeded the maintenance SAA requirement, the excess being available for keratin synthesis. We can only conclude from these data that a primary implication of the "aminostatic hypothesis" was not expressed by the birds in our experiments; i.e., food consumption was unaffected through a range of dietary SAA and cyst(e)ine concentrations that occur in natural foods (based on our estimates from data contained in F.A.O. [1970]) and that also brackets the requirements of poultry for these amino acids (National Research Council 1977).

We turn next to an examination of correlations, or lack of them, among other components of energy intake, flow, and excretion. Food consumption was inversely correlated with the energy utilization coefficient (Fig. 1). Decreasing trends in food consumption (stage 1 significantly > stage 7 in all dietary groups) were accompanied by increasing trends in the UC (stage 1 significantly < stage 7 in all groups). Because the diet × stage interaction was not significant ($P = 0.0850$) for the UC, the main effects of diet and stage could be considered separately (Table 3). Differences in the mean UC of the five groups were marginally significant ($P = 0.0655$), and there were no clear-cut relationships between diets in the utilization of energy as expressed through the UC. For example, the UC in birds consuming diet A (lowest SAA and cys concentrations) differed significantly from those consuming diet D (highest) only in stage 1 and was consistently higher than in diet C throughout molt. Differences of UC among molt stages for all groups, however, were highly significant ($P = 0.0001$) even though relatively small (ca. 72 and 86% at the extremes), with an upward trend through time. Although perhaps confounded by a partial correlation with gross energy consumption, this trend may also reflect merely a progressive acclimation of the birds to the synthetic diets. Chilgren (1975) did not find trends of UC during molt in White-crowned Sparrows that were fed chick-starter mash. Whatever its cause, this trend in our experiments does not reveal an association between the efficiency of food utilization and the intensity of molt. The increase of the UC resulted from significant decreases (stage 1 > stage 7 in all groups) of total excreta/day and in the caloric density of the excreta (and hence in total excretory energy loss/day: Fig. 2), presumably permitting energy demands to be met by decreasing quantities of food. The interrelations of these variables suggest that energy demand rather than SAA demand is the prepotent regulator of food consumption.

Finally, we consider the net energy cost of molt and the changes of body weight during molt (Fig. 3). The patterns of body-weight variation were consistent among the diets and also with the patterns reported by Chilgren (1977) in White-crowned Sparrows fed chick-starter mash and subjected to various air temperatures. Because of this concordance we have reported metabolized energy without attempting to make corrections for body-weight variation. We did, however, undertake a preliminary analysis of metabolized energy corrected for body-weight variation, using 29 and 17 kJ/g as the caloric equivalents of weight gain and loss, respectively. The results were largely unaffected, probably for two reasons. First, weight changes through any three-day trial were usually small (typically less than 0.5 g). Second,

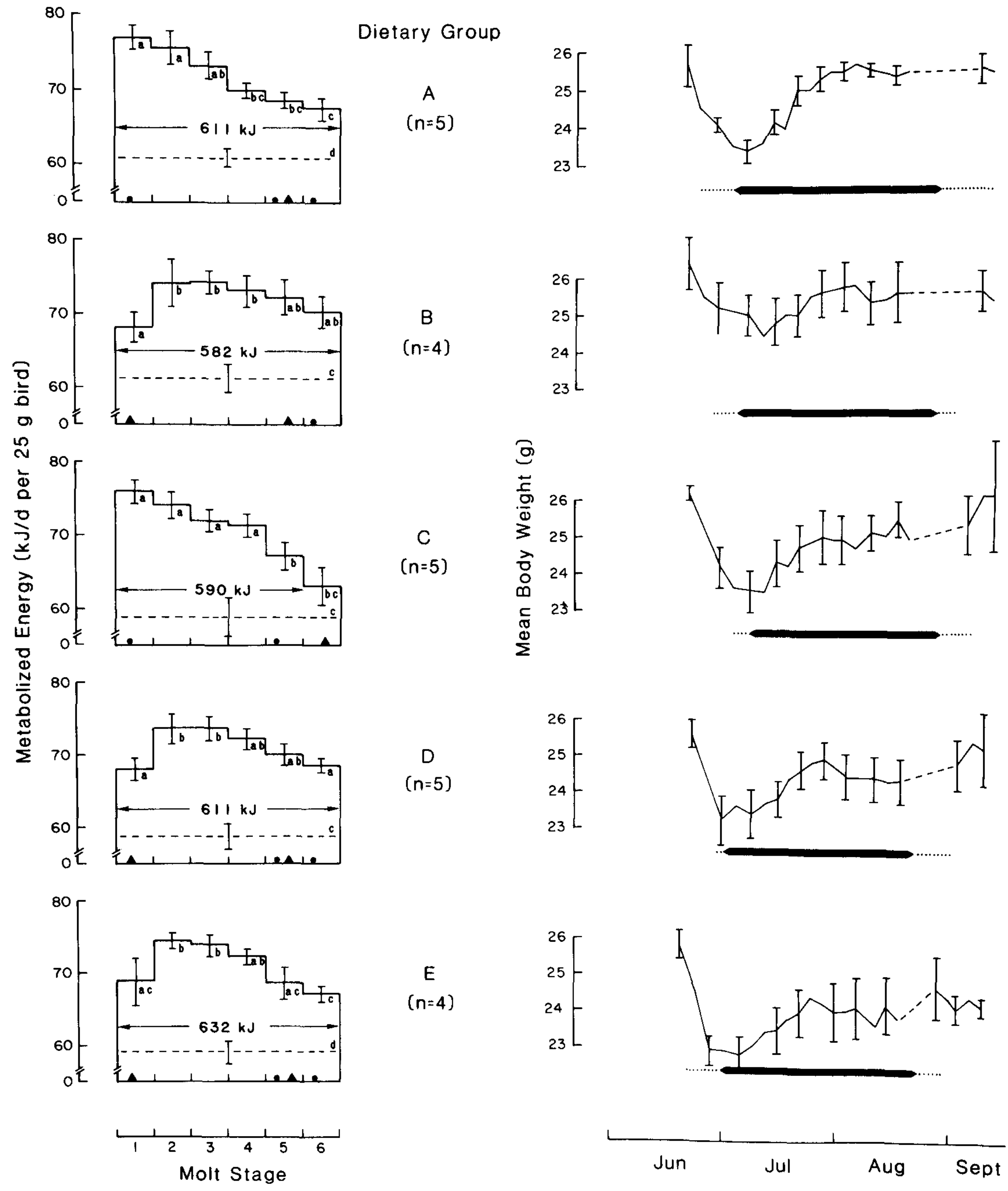

FIGURE 3. Mean (±SE) metabolized energy (ME) and body weights through molt and in non-molt. Standard-error bars for body weights are shown only with alternate means to avoid clutter. The shaded horizontal bars (right panel) show the period of molt. Stages within histograms that have the same lower-case letters (compare horizontally) do not differ ($P > 0.05$). Stages between histograms that have the same symbol (circles, triangles) or that lack symbols (compare vertically) do not differ ($P > 0.05$). Basal ME is shown by a dashed line.

the patterns of weight variation were so similar in all groups that "corrections" for the changes had little or no effect on the comparative results. This being so, we preferred to base our analysis on measured values rather than values "corrected" on the basis of questionable conversion factors (King 1972).

We sought to minimize dependence on the estimate of basal or maintenance metabolized energy expenditure (equal to stage 7) in evaluating the differences of metabolized energy income among the dietary groups; therefore, we compared the total (rather than net) metabolized energy by molt stages. Because the interaction of stage × diet was significant ($P = 0.0004$), the main effects of diet and stage could not be considered separately. Comparisons of all means by Duncan's Multiple Range Test (alpha = 0.05) revealed significant differences among diets only in stages 1, 5, and 6 (compare symbols vertically in Fig. 3). These included only diet A or C as compared with B, D, or E in stage 1, and B as compared with C in stage 5, and C as compared with the other groups in stage 6. The differences in stage 1 (observed also in food intake) probably resulted from the net increases of body weight by birds of groups A and C (0.16 and 0.51 g, respectively), as contrasted with the fairly stable or slightly decreasing weights in this stage by the birds of groups B, D, and E (−0.62, −0.30, and −0.51 g, respectively: Fig. 3). Substantial variability of body weight in this stage of molt is not unusual and was actually less in our experiments than that reported by Chilgren (1977) among groups of White-crowned Sparrows that all consumed identical diets. We suspect that weight changes might also account for the differences in metabolized energy noted between groups B and C through stage 5. It is not unlikely, of course, that some "significant" differences will simply be fortuitous in intricate multiple comparisons such as these.

In all but group C (stages 1–5 but not stage 6) the basal metabolized energy (=stage 7, postmolt) was significantly less ($P = 0.05$) than in stages 1–6 (molt). The net energy cost of molt as estimated from the areas bounded by the histograms in Figure 3 ranged from 582 kJ in group B to 632 kJ in group E. We compared these measured values with those estimated by the aminostatic equation when using empirical values as its variables (Table 4). The large discrepancies between measured and hypothetical results indicate that in White-crowned Sparrows the availability of dietary SAA, and less so of cyst(e)ine alone, regardless of the efficiency of utilization, has little effect (if any) on the net energy cost of molt. The aminostatic equation thus seems to be unreliable at least in this species.

In short, the White-crowned Sparrows in our experiments were able to sustain a normal molt without differences of gross food intake among dietary groups when consuming diets that contained as little as 0.33% SAA (with cyst(e)ine representing only 0.2% of dietary protein) and as much as 0.78% SAA. This was so in spite of the progressive increase of the UC in all groups, an increase that acted to minimize or even obscure the increase of food intake (and thus of SAA) that would normally accompany increased energy demands. Paradoxically, an increase of the UC, while superficially suggesting an increase of efficiency in the use of nutrients, may actually be detrimental if it results in a reduction of food intake and hence in a reduction in the intake of substrates required in molt, or any similar productive process. This is implicit in the suggestion by Thompson and Boag (1976) that the increase of food intake (energy) associated with molt automatically increases the income of essential nutrients, and is demonstrated by the data of Gavrilov (1974). He found that the quantity of food necessary to support the energy demands of molt in *Passer domesticus* and *Fringilla coelebs* supplied an amount of **cyst(e)ine** equal to that contained in the plumage. Because methionine is typically more concentrated than cyst(e)ine in the mixed proteins of foods (F.A.O. 1970), the amount of additional SAA consumed during molt probably exceeded by two-fold that deposited in the plumage.

TABLE 4. Predicted (aminostatic equation) and measured net energy cost of molt (*NEM*) in relation to diet.

	Net energy cost of molt (kJ)				
	Predicted[a]				
	Cys utilization		TSAA utilization		
Diet	100%	68%	100%	68%	Measured
A	8,395	12,346	818	1,203	611
B	1,188	1,747	503	740	582
C	632	929	364	535	590
D	464	682	309	454	611
E	8,354	12,285	388	571	632

[a] Calculated according to the aminostatic equation: $W_{pl} = 1.75$ g (Chilgren 1977), $A_{pl} = 91$ mg/g dry weight (Murphy and King 1982a), *GEI* = 17.4 kJ/g dry weight, *MEC* (= UC) for the diets = 81.8 (A), 78.7 (B), 77.5 (C), 83.4 (D), 81.4 (E). A_{pr} was calculated according to the compositions of the respective diets (Table 1), with moles of methionine converted to equivalent mg of available cyst(e)ine. 100% and 68% "utilization" represent limits in the use of dietary SAA in keratin synthesis.

Lastly, we consider briefly the apparent net energy cost of molt and the net efficiency of production. King (1981) noted that the reliability of energy-balance methods, such as the one used in this investigation, depends on fulfillment of the assumption that energy expenditure in locomotor activity is invariant through the test period (premolt, molt, and postmolt). Chilgren (1975) showed that this was not so in White-crowned Sparrows, and that locomotor activity decreased sharply during the postnuptial molt compared with activity in pre- and postmolt periods. This is evidently true in several other species of finches (Eyster 1954). For comparative purposes we assumed, as seems reasonable in view of the concordance of other variables, that locomotor activity varied in parallel through molt in all five dietary groups in our experiments. Nevertheless, the grand average *NEM* is likely to be an underestimate of the true *NEM* because of the putative reduction of energy diverted to locomotor activity. The mean *NEM* did not differ significantly ($P = 0.05$) among the five groups, and the pooled mean (±SE) was 605 ± 38 kJ/25-g bird ($n = 23$). This is substantially less than the average of 821 kJ (469 kJ/g of plumage × 1.75 g of plumage) estimated by King (1981) for small birds, including the White-crowned Sparrow. This finding prompts us to reiterate his caveat that "it cannot be emphasized too strongly that these measurements [of *NEM*] are still subject to a substantial uncertainty, and should not be petrified as dogma."

The apparent net energetic efficiency of feather synthesis in this investigation was 6.4% [100(1.75 g of plumage × 22 kJ/g)/(605 kJ/plumage)], and did not differ significantly among groups. This quantity may be overestimated because of the putative underestimation of the *NEM,* but still would appear to be far less than the net energetic efficiency of other kinds of productive processes (as we discussed earlier in this report). This calls for an explanation of the fact that so little of the metabolized energy associated with molt is deposited in the plumage. We can only speculate about this. The explanation does not seem to lie in increased thermoregulatory costs entrained by the shedding and regrowth of plumage, because this investigation as well as most other ones like it were conducted at thermoneutral air temperatures. On the contrary, Gavrilov and Dolnik (1974) argued that the dissipation of heat at moderate to high air temperatures is more challenging to molting birds than the production or conservation of heat for thermoregulation. An alternative explanation for the apparently large energy cost of molt compared to the energy deposited in plumage was sketched by Hanson (1962) and proposed by Dolnik (1967: as cited by Gavrilov and Dolnik 1974). They suggested that molt entrains a generalized acceleration of protein metabolism beyond that associated with the synthesis of keratin, and that a large amount of energy may be devoted to supporting additional, and apparently obligatory, protein synthesis. We are currently initiating experiments to examine this postulate.

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