males when pair formation and courtship occur (e.g.
Tinbergen 1959), facilitating copulation. Whether
adult males are submissive for this reason or for the
reason proposed by Smith (1980), yearling males still
are able to exploit the system and gain access to space.

I thank the Robert Erickson family, especially Car-
rie, for their generous hospitality while I was in Ar-
izona and Carrie Erickson for her help in the field.
Mary Bomberger, John Hoogland, Sievert Rohwer,
and Dan Rubenstein made helpful comments on the
manuscript. My parents, Raymond and Kathryn
Brown, financially supported this research.

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Dietary Sulfur Amino Acid Availability and Molt Dynamics in White-crowned Sparrows

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Although pitifully little is known about how the
patterns of avian molt are controlled (Payne 1972), it
is at least arguable on reasonable grounds that the
rate and sequence of feather replacement are domi-
nated by a genetic program. In the first place, molt
patterns (ordination of replacement within pterylae,
coordination among pterylae) are nearly invariant
within major phyletic lines (Stresemann and Strese-
mann 1966), which implies that they are conservative
traits that were fixed early in evolution. In the
second place, the experimental investigations by Me-
waldt and King (1978) of 12 populations of White-
crowned Sparrows (*Zonotrichia leucophrys*) from var-
ious latitudes (35–49°N) showed that the duration of
the postnuptial molt was progressively shorter
northward, even though the birds from all popula-
tions were kept during molt in the same environ-
mental conditions at an intermediate latitude. This
implies a strong genetic component. Nevertheless, it
is evident also that the genome that controls molt is
sensitive to extrinsic influences, no doubt mediated
by the neuroendrocine system, within a moderate
range of plasticity. For instance, the postnuptial molt
may be temporarily suspended by a late nesting cycle
(King 1972), may be abbreviated in birds whose nest-
ing season was prolonged by renesting following
predation (Wingfield and Farner 1979), and, in ex-
perimental situations, may be modified in duration

within a relatively narrow range by air temperature
or photoperiod (Gavrilov and Dolnik 1974, Chilgren
1978). Finally, the availability of nutrients has been
frequently invoked as an actual or potential modifier
of the course of molt. The amino acid cystine, be-
cause of its relative abundance in feathers (Murphy
and King 1982a) and its importance in the structure
of keratin, has frequently been cited as a potentially
limiting nutrient in the growth of plumage (Hanson
1962, Newton 1968, Ward 1969, Gavrilov and Dolnik
1974). Although it has been found in some investi-
gations that the rate of wool growth in domestic sheep
(Reis and Schinckel 1963, Reis 1965) and of hair
growth in the laboratory rat (Smuts et al. 1932) is
enhanced by increased dietary sulfur amino acid
(SAA) intake, the correlation of the rate of feather
growth with SAA intake by domestic fowl is equiv-
ocal [Ackerson et al. 1928 (and references cited there-
in); Taylor and Russell 1943, Brake et al. 1979].

To test the foregoing hypotheses and speculations,
we measured the rates of feather elongation, the
shedding interval between remiges, the temporal co-
ordination between remigial tracts, the duration of
the molt, and the renewed feather mass in groups of
White-crowned Sparrows that were fed diets differ-
ing in cystine and methionine content. The main
purpose of these experiments was to characterize en-
ergy expenditure and nitrogen and sulfur balance

TABLE 1. Relationships among diets and measures of postnuptial molt.

Variable	Dietary groups[a]							df	P[b]
	1	2	3	4	5	6	7		
SAA									
As % of diet[c]	0.28	0.33	0.48	0.63	0.69	0.78	0.83	—	—
As % of protein	2.15	2.50	3.66	4.82	5.30	5.99	6.43	—	—
MOLT									
Duration (days)[d]	—	56	55	53	54	50	—	4,19	0.592
Growth rate (mm/day)									
P1	—	3.4	3.4	3.5	3.4	3.5	—	4,19	0.754
P7	3.5	3.6	3.6	3.6	3.6	3.6	3.6	6,28	0.876
Shedding interval (days)									
P4–P7	—	13.6	13.2	11.8	13.5	10.2	—	4,18	0.270
P1–S1	—	21.4	21.3	20.6	19.0	18.9	—	4,18	0.564
Plumage mass (g)[e]									
Body feathers	1.54	—	—	—	—	—	1.69	7	0.170
Remiges	0.32	—	—	—	—	—	0.30	7	0.165
Rectrices	0.17	—	—	—	—	—	0.15	7	0.239
Total	2.03	—	—	—	—	—	2.14	7	0.251

[a] Range of cystine as % protein = 0.2% (diets 1, 2, 5) to 3.7% (diet 7); range of methionine as % protein = 1.9% (diet 1) to 5.1% (diet 5).
[b] Probability that group means are homogeneous (ANOVA for duration, growth rate, shedding interval) or differ (paired t-test for plumage mass).
[c] Percentage of dry weight (all diets = 13.5% protein by dry weight).
[d] Duration of remigial growth.
[e] Air-dried plumage.

during molt (Murphy and King in press a, b). A detailed description of molt is not germane to our separate reports on these subjects, and so we therefore present here a brief account of our findings on the effects of dietary sulfur-containing amino acids (SAA) on the dynamics of molt.

We captured White-crowned Sparrows (*Z. l. gambelii*) during their migration through eastern Washington and kept them in an outdoor aviary where drinking water and chick-starter mash (20.7% protein, 74.7% carbohydrate, 3.1% fat, and 1.5% ash) were freely available. We undertook two series of experiments. About 1 month before the postnuptial molt started, we transferred the experimental birds from an outdoor aviary to constant-condition rooms (21°C, LD 16:8) and put them in individual cages (22 × 40 × 27 cm). These birds (4–5 in each group) were fed diets 2 through 6 (Table 1) continuously through a 1- to 3-week premolt period, for the duration of molt, and through a 2- to 4-week postmolt period. Later, we deemed it necessary to extend the dietary series to very low (diet 1) and very high (diet 7) concentrations of SAA, and so we repeated the experiment using a second group of birds that were fed these two diets. The seven semi-synthetic diets were based on the maintenance ration described by Murphy and King (1982b), but with graded concentrations of cystine and methionine. These amino acids are reported together as total sulfur-containing amino acids (SAA) in Table 1.

The seven diets were isocaloric (17.40 kJ/g = 4.156 kcal/g dry wt.) and were rendered isonitrogenous by adjustments of their glutamic acid concentrations. The SAA concentrations of this series bracketed the requirements of laying poultry (National Research Council 1977) and correspond to the range of mean total SAA concentrations (as % protein) in various plant and animal foodstuffs that we calculated from data compiled by the FAO (1970). The range of cyst(e)ine concentrations of the test diets exceeded the range of averages in natural foods. Methionine concentrations in the test diets ranged from slightly greater than the averages found in some plants to much greater than those found in animals and animal products.

We measured the length of every growing primary and secondary remige (flattened, to the nearest 0.5 mm) at 3-day intervals in the birds of dietary groups 2–6 and at 6-day intervals in groups 1 and 7. To assess the reliability of these measurements we measured the length of the first primary remige (P1) for 8–10 intervals after it had attained its full length in 10 birds. The coefficients of variation ranged from 0.71 to 1.03%. The elongation of the remiges, at least after the pinfeather emerges from the skin and its length becomes measureable, most clearly approximates a von Bertalanffy growth curve, without the initial inflexions of accelerating growth that characterize logistic and Gompertzian curves (Ricklefs 1967). The initial limb of the von Bertalanffy curve is nearly linear, and so we estimated the growth rates of selected primary remiges by progressively deleting data points from right to left at the upper inflexion of the curve until reiterated least-squares linear regressions of length on time produced a maximum slope.

We used the period between the first appearance

of P1 beyond the skin and the attainment of full growth by P9 as a comparative estimate of the duration of molt in groups 2–6. We could not estimate duration in groups 1 and 7, because (owing to compromises in a heavy schedule of more crucial measurements) recording was not initiated until the molt had reached about P2–P4. Because the duration of molt depends not only on the growth rates of individual feathers but also on the intervals of time between the shedding of successive feathers, we also estimated shedding intervals between P4 and P7 and between P1 and S1 as arbitrary comparative indices. If a new pinfeather emerged from the skin during the 3-day interval between observations in groups 2–6, we estimated the day of initial growth by extrapolating backward from its measured length and its linear growth rate as defined by later measurements of the same feather. In groups 1 and 7 we measured the remiges at 6-day intervals and felt that such extrapolation would compound error unacceptably. We therefore lack data on the shedding intervals in these groups.

Finally, to find out whether or not the renewed plumage mass is related to dietary SAA, we sacrificed the birds fed the lowest (diet 1) and highest (diet 7) concentrations of SAA, plucked them, and weighed the air-dried new plumage from each individual. Because differences between the means of the two groups might be caused simply by chance differences in body size, we compared both the mean body weights and standard errors (27.4 ± 2.15 g and 26.1 ± 1.67 g in groups 7 and 1, respectively) and the mean lengths of P1 and standard errors (54.8 ± 1.16 mm and 55.7 ± 1.03 mm, respectively) and found no significant difference by t-test ($P > 0.05$). We therefore regard the birds in groups 1 and 7 to be alike in body size.

The pattern of postnuptial molt in all of the experimental groups (Table 1) closely resembled that found by Chilgren (1978) in *Z. l. gambelii* exposed to several air temperatures and photoperiods but fed chick-starter mash. For instance, Chilgren reported that the duration of growth in the remiges was 50–56 days and that the P4–P7 shedding interval was 11.0–12.8 days, as the range of averages in four indoor groups.

Because of their small range of variation in relation to dietary SAA, it is scarcely necessary to invoke statistical tests to reject the hypothesis that our indices of molt dynamics are correlated with dietary SAA. Nevertheless, one-way ANOVA (duration, growth rate, shedding interval) or t-test (plumage mass) reveals that there is no significant heterogeneity among group means in any of our measures of molt pattern (Table 1). Thus, rates of feather growth (P1, P7), shedding interval within tracts (P4–P7), coordination among major tracts (P1–S1), duration of molt, and new plumage mass are unrelated to the broad range of dietary concentrations of SAA examined in this

investigation. Close inspection of Table 1, however, reveals some vague correlations between the duration of molt, shedding intervals, and dietary SAA concentrations. These apparent dietary trends are not significant when tested by regression analysis (duration vs. diet: $r^2 = 0.107$, $P > 0.05$; P4–P7 shedding interval vs. diet: $r^2 = 0.132$, $P > 0.05$; P1–S1 shedding interval: $r^2 = 0.116$, $P > 0.05$). The P4–P7 and P1–S1 shedding intervals, however, are significantly correlated to the duration of molt (by Spearman's rank correlation test, $P < 0.01$ and $P < 0.01$, respectively). Because the growth rates of feathers are essentially invariant across diets, the slight variation in molt duration among individuals must therefore result from variation in the intervals at which feathers are shed. This suggests that normal variation in the pace of molt in bird populations is more likely to be controlled by the intervals at which growth is initiated in successive follicles (which also determines the shedding interval: Watson 1963) than by modification of growth rate.

The major point emerging from our experiments, however, is that the dynamics of molt are unaffected by diets in which SAA concentrations range beyond the extremes of SAA concentrations in the natural foods typically eaten by granivorous birds. These results suggest that SAA limitation per se (if it exists at all) is an exception, rather than the rule, in the proximate regulation of molt dynamics in nature. Even if a cystine shortage should occur during molt, we hypothesize through analogy with investigations of growing rats (Tateishi et al. 1977, Cho et al. 1980, Seligson and Rotruck 1983) and domestic fowl (Goto and Okamoto 1965) that White-crowned Sparrows and other birds may possess the capacity to rely partially on cysteine reserves such as the tripeptide glutathione (glu-cys-gly) and may even increase these supplies in "anticipation" of molt. Such a reserve would ensure a cysteine source to support keratin synthesis during the overnight period of fasting or through short-term SAA deficits. In the case of long-term dietary SAA inadequacy a compensatory reduction in tissue glutathione might permit diversion of adequate amounts of incoming SAA to feather synthesis, thus sparing tissue protein and sustaining feather growth.

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