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Received 27 December 1985, accepted 4 April 1986.

Composition and Quantity of Feather Sheaths Produced by White-crowned Sparrows During the Postnuptial Molt

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Measures of nitrogen balance and sulfur balance in molting White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) revealed that the new plumage mass accounted for only about 50% of the nitrogen, and only about 80% of the sulfur, retained above the maintenance level during the molt (Murphy and King 1984a, b; corrected to a regenerated plumage mass of 2.1 g). These discrepancies result from undetected sites of nitrogen and sulfur deposition during molt or from nonquantified losses from the body. Included among the potential routes of deposition and undetected loss of nitrogen and sulfur are the sheaths that temporarily encase the growing feathers (Murphy and King 1984a). A sheath is a keratinized epithelial tube (Lucas and Jamroz 1961) that protects the pulp and growing feather from desiccation. It may help initially to retain the feather in its follicle, and function in the elongation of feather barbs (Lillie 1940). Sheaths are ephemeral. They rupture when the growing feather reaches about 20% of its final length, and soon thereafter begin to disintegrate from the tip into small flakes. Probably because they are short-lived and difficult to collect, sheaths have been essentially disregarded in analyses of the nutritional requirements of molt. To help remedy this lapse, we analyzed sheath chemical composition and attempted to estimate the mass of sheaths produced during the complete postnuptial molt of White-crowned Sparrows.

We captured White-crowned Sparrows during their spring migration through eastern Washington and kept them in an outdoor aviary where chick-starter mash and fresh water were freely available. During the postnuptial (late summer) molt, we plucked samples of growing feathers from the alar (primaries, secondaries, greater coverts), caudal (rectrices), and

TABLE 1. Feather masses, sheath masses, and derivation of factors to estimate the mass of intact sheaths (mean ± SD).

Quantity	Feather type			
	Primaries	Secondaries	Greater wing coverts	Spinal tract contours
Sheath mass (mg/feather)	1.60 ± 0.22 (n = 75)	0.94 ± 0.22 (n = 94)	0.34 ± 0.03 (n = 9 × 20)	0.14 ± 0.01 (n = 9 × 100)
Feather mass (mg/feather)	10.56 ± 1.69 (n = 5 × 9)	6.96 ± 0.85 (n = 5 × 7)	1.77 ± 0.16 (n = 5 × 10)	1.09 ± 0.06 (n = 5 × 10)
Uncorrected sheath/feather	0.151	0.135	0.192	0.128
Intact sheath length[a] (mm)	18.7 ± 1.02 (n = 30)	19.25 ± 1.81 (n = 94)	nd[b] —	nd —
Separated sheath length (mm)	15.0 ± 2.15 (n = 75)	12.98 ± 2.42 (n = 94)	nd —	nd —
Correction factor[c]	1.25	1.48	1.36[d]	1.36[d]
Corrected mass, sheath/feather	0.189	0.200	0.261	0.175

[a] Including an estimated 1 mm lost during natural rupturing of the sheath.
[b] Not determined.
[c] Intact length/separated length.
[d] Average of remigial factors.

spinal tracts. The length of the feather and its intact sheath were recorded in the case of flight feathers, and the length of the separated sheath was measured later. An "intact" sheath is one that is still encasing its feather, although it may be ruptured at the tip, and a "separated" sheath is one that has been dissected from the feather and washed. We separated the pulp and growing feather from the sheath by first tugging exposed parts of the feather vane out of the sheath. Then we inserted a hypodermic needle of appropriate gauge into the emptied sheath and cut it lengthwise with the sharpened edge of a second needle. We could then open the sheath and scrape its inner surface clean. Sheaths were washed (Harrap and Woods 1964), air-dried, and weighed individually to the nearest 0.05 mg. We likewise weighed mature remiges (primaries and secondaries), spinal contour feathers, and greater wing coverts collected from recently molted White-crowned Sparrows. Coverts and spinal contours were weighed in batches of 10 of each, and the separated sheaths were weighed in batches of 20 and 100, respectively. Later, we analyzed samples of finely cut sheaths for nitrogen content (micro-Kjeldahl method according to Horwitz 1980) and amino-acid composition (Beckman model 121 MB, Bioanalytical Laboratory, Washington State Univ.). For details, see Murphy and King (1982).

To estimate the total mass of sheaths produced during the molt, we determined the ratio of sheath mass to feather mass in four feather groups (primaries, secondaries, wing coverts, and spinal contours). To account for small bits of sheath that flaked off during the normal eruption of the feather, and other bits that were unavoidably lost during cleaning of the sheaths, we generated a correction factor equal to the mean intact sheath length divided by the mean separated sheath length. We multiplied the measured sheath mass by this correction factor to obtain a sheath mass corrected for losses.

We estimated that White-crowned Sparrows during their postnuptial molt generate a total mass of feather sheaths (ca. 380–420 mg) equivalent to at least 18–20% of the mass of the new plumage (ca. 2.0 g; Murphy and King 1984b). This is a conservative estimate because the correction factor for loss of sheath material was based on the larger and sturdier remigial sheaths (Table 1). Our dissection of the smaller, more delicate sheaths of the spinal contour feathers probably entailed a slightly greater proportional loss than in the remiges, and use of the correction factor probably underestimates the amount of sheath produced. Nevertheless, the estimate of sheath mass as 18–20% of the new plumage mass is accurate enough to show that the synthesis of feather sheaths requires a quantity of nutrients that should not be overlooked in assessing the nutritional requirements of molting birds.

Chemical analysis of sheaths showed that they, like feathers, are largely proteinaceous. Their mean (±SD, n = 3) nitrogen content was 15.16 ± 0.09% by mass, which is essentially indistinguishable from the 15.22% nitrogen content of White-crowned Sparrow feathers (Murphy and King 1982). The amino acid composition of sheaths (Table 2) differed, however, from that of homogenized plumage and of feather calamus (Fig. 1). This is consistent with the observation by Rudall (1947) that x-ray diffraction analysis of thin sheath material from the calamus of a domestic goose yields the "α-pattern" of keratin, while all other parts of the feather yield the "feather-pattern." Avian epi-

TABLE 2. Mean amino acid composition of feather sheaths.

Amino acid[a]	μmoles/g		mg/g		cv[b]
	Remiges	Contours	Remiges	Contours	
Essential					
Arginine	371	390	58.0	61.0	4.3
Histidine	54	58	7.4	8.0	4.7
Isoleucine	264	232	29.8	26.3	6.4
Leucine	702	658	79.4	74.4	8.1
Lysine	259	275	33.2	35.2	7.3
Methionine	54	66	7.1	8.7	5.5
Cystine/2	577	605	58.9	61.8	6.0
Phenylalanine	284	297	41.8	43.7	8.1
Tyrosine	264	280	43.0	45.6	7.5
Threonine	264	272	26.7	27.5	6.8
Tryptophan	nd[c]	nd	nd	nd	—
Valine	464	480	46.0	47.6	7.3
Nonessential					
Alanine	832	834	59.1	59.2	6.6
Aspartic acid	424	457	48.8	52.6	4.2
Glutamic acid	838	813	108.2	105.0	8.8
Glycine	1,160	1,259	66.2	74.1	9.8
Proline	902	910	87.5	88.3	4.5
Serine	493	463	42.9	40.3	5.1
NH_3 released	1,174	1,263	20.0	21.5	15.6
Percentage accounted for:					
Nitrogen	99.9	103.0			
Mass	86.4	88.1			

[a] Uncorrected for destruction during hydrolysis; n = 6 birds for remiges, n = 1 bird for contour feathers. Amino acid concentrations in contour sheaths are within the range of concentrations measured in remigial sheaths.

[b] Coefficient of variation for remiges.

[c] Not determined.

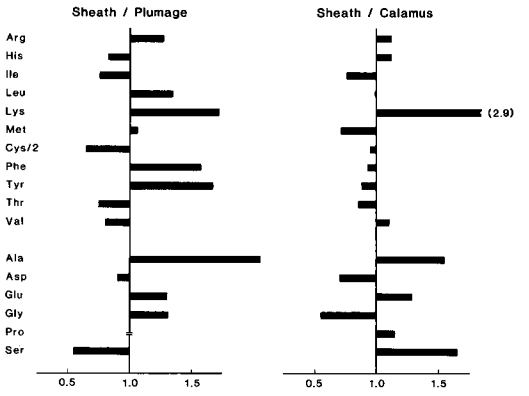

Fig. 1. Relative amino acid composition of feather sheaths and of whole plumage and calamus, shown as the ratio of molar concentration in sheath to molar concentration in plumage or calamus. Concentrations were equal (ratio = 1.0) only in proline in sheath and plumage. All other amino acids were either less concentrated (ratio <1.0) or more concentrated (>1.0) in sheaths than in other feather parts. Analyses of all samples were uncorrected for destruction of amino acids during hydrolysis (about 3% threonine and about 6% serine; Rattenbury 1981: 129). Direct comparisons were considered justified by the less than 5% variability in total μmoles of amino acid per gram of the various materials. Likewise, masses of amino acids per gram of plumage, calamus, and sheath were similar (832, 850, and 864 mg/g, respectively). Differences in percentage mass accounted for by constituent amino acids is largely attributable to variabilities in the molecular weights of constituent amino acids. All calculations were based on dehydrated molecular masses.

dermis likewise yields the α-keratin pattern (Fraser et al. 1972), as would be expected in view of the similar histological origin of epidermis and sheath (Lucas and Stettenheim 1972). The disparities of amino acid composition among sheaths, calamus, and whole plumage were greatest in lysine, phenylalanine, tyrosine, alanine, glycine, and serine. There do not appear to be trends of difference in essential vs. nonessential amino acids. Cyst(e)ine concentrations in sheaths and calamus were similar, but were only about two-thirds of the concentration found in homogenized whole plumage. This is attributable to the typically higher concentration of cyst(e)ine in barbs than in other feather parts (Murphy unpubl. data). We surmise that the differentiation of feather parts in respect to the type or types of keratin [and hence the amount of cyst(e)ine] that they contain reflects the demands of their mechanical functions. The sheaths, fated to split at an appropriate stage and then be preened away, are constructed from relatively lower cyst(e)ine keratins.

The production of sheaths during molt entails the deposition of about 1.13 mg of nitrogen (N) (about 7 mg protein) per day [(380 mg sheath/54 days) × 0.1516 N], but can approach twice this amount at peak molt. Nitrogen deposition as sheaths during molt therefore is equivalent to 19–38% of the daily endogenous nitrogen loss of a nonmolting White-crowned Sparrow (6 mg N/day, calculated from Robbins 1981). When nutrition is adequate (high-quality protein), and assuming ca. 100% metabolic efficiency, sheath synthesis would increase maintenance protein requirement (27 mg N/day, calculated from Robbins 1981) by *at least* 4–8% per day.

The *net* nitrogen retention of molt averages about

11.5 mg N/day, which is 43% above maintenance retention. Feather synthesis accounts for the retention of roughly 6.0 mg N/day [(2.0 g of new plumage plus a correction factor of 105 mg for replacement of rectrices damaged and lost during growth) multiplied by 0.1522 N; Murphy and King 1984a, b]. Synthesis of sheaths adds appreciably to this quantity and accounts for at least an additional 10% of the nitrogen retained during molt. About 4 mg N/day retained during molt is still not accounted for quantitatively. Some of it undoubtedly is deposited in other integumentary structures that are renewed during the molt, and in accessory structures such as pulp, increasing numbers of erythrocytes, increases in peptide stores (Murphy and King 1985), and perhaps in accretion of other body proteins.

This investigation was supported by a grant from the National Science Foundation (BSR 8207511). We thank S. Gurusiddaiah, Associate Director, Washington State University Bioanalytical Laboratory, for his assistance and helpful discussions, and C. J. Costa for helping to capture the birds.

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Received 13 November 1985, accepted 15 April 1986.

Note Added in Proof

Analysis of feather parts completed after this report was in press suggested larger losses of serine during hydrolysis than reported by Rattenbury (1981). By analyzing the amino acid composition of samples of rachis hydrolyzed from 12 to 24 h, we found that as much as 35% of serine and 14% of threonine was destroyed between 12 and 24 h. The other amino acids were stable. We used 24-h hydrolysates in the analysis reported in Table 2.

Estimating Nest Detection Probabilities for White-winged Dove Nest Transects in Tamaulipas, Mexico

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Nest transects in nesting colonies provide one source of information on White-winged Dove (*Zenaida asiatica asiatica*) population status and reproduction. Nests are counted along transects using standardized field methods each year in Texas and northeastern Mexico by personnel associated with Mexico's Office of Flora and Fauna, the Texas Parks and Wildlife Department, and the U.S. Fish and Wildlife Service. Nest counts on transects are combined with information on the size of nesting colo-