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AMINO ACID COMPOSITION OF FEATHER BARBS AND RACHISES IN THREE SPECIES OF PYGOSCELID PENGUINS: NUTRITIONAL IMPLICATIONS[1]

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Abstract. To evaluate the nutritional challenge faced by molting penguins we studied the composition of contour feathers of three species of penguins, *Pygoscelis adeliae, P. antarctica,* and *P. papua.* The feathers of these species are nearly identical in structure and chemical composition. They have a unique broad, flat rachis that accounts for 60 to 70% of the total feather mass. Their barbules are pennaceous and able to interlock tightly, which probably accounts for the shedding of plumage in sheets rather than as individual feathers. Compositionally, the penguin feathers are remarkably similar to feathers of other species of birds representing six different orders and varied life-styles. Whole penguin feathers averaged 8–10% water. Ash contents of *P. adeliae* and *P. antarctica* feathers averaged less than 1%, but *P. papua* averaged 2.6%. The nitrogen contents of the barbs were nearly identical in the three species and averaged 16.4%. The nitrogen content of the rachises of *P. adeliae* and *P. antarctica* feathers averaged 16.4%, but was slightly less in *P. papua* (15.5%), probably due to the higher ash content and slightly higher pigment content in this species. The most abundant amino acids in barbs and rachises were gly, pro, ser, cys/2, val, and leu. Six nonessential amino acids (ala, asp, glu, gly, pro, ser) made up 52.5 and 54.3% of the barbs and rachises, respectively. The basic amino acids (lys, his, arg) were among the least concentrated amino acids. This amino acid profile is typical of mixed feather keratins. The high cys/2 contents of feather proteins results in a large mismatch between nonkeratinous mixed tissue proteins and feathers that could result in highly inefficient reutilization of tissue amino acids in feather synthesis during the molt fast. Some compensatory mechanisms that penguins might use to minimize this inefficiency are discussed.

Key words: Penguins; molt; feather composition; feather structure.

INTRODUCTION

A complete molt—the renewal of the feathers and other parts of the integument—is one of the most remarkable metabolic feats that birds undergo during the course of their annual cycle. A complete molt involves the synthesis of an amount of epidermal proteins (largely keratins) equal to at least a quarter of the total protein mass of a bird's body (Mitchell et al. 1931, Newton 1968, Myrcha and Pinowski 1970, Gavrilov and Dolnik 1974, Chilgren 1975, Carey et al. 1978), often in a short period of time. The epidermal proteins are notably rich in the sulfur-containing amino acid cystine. Feather proteins contain proportionately more cystine than most other tissue proteins and most food proteins (Bloch and Bolling 1945, Kuppuswamy et al. 1958, FAO 1970, Murphy and King 1982). For decades, biologists have noted this mismatch and have investigated its potential limitations on rates of keratin synthesis (e.g., Ackerson et al. 1926; Ackerson and Blish 1926; Smuts et al. 1932; Taylor and Russell 1943; Mitchell 1959; Reis and Schinkel 1963; Newton 1968; Reis et al. 1973; Gavrilov and Dolnik 1974; Brake et al. 1979; Murphy and King 1984a, 1984b, 1985, in press; Andrews et al. 1987; Murphy et al. 1988). Furthermore, variation of dietary SAA ("sulfur amino acids" = cyst(e)ine + methionine) availability has often been invoked as a potential explanation for observed changes in feeding habits, body composition, and even the energy budgets of wild birds during molt (e.g., Hanson 1962; Newton 1968; Ward 1969; Gavrilov and Dolnik 1974; Murphy and King 1984c, 1987). All the aforementioned studies involved animals that normally feed when regenerating their integument. In penguins, which fast during much of the molt, the effect of the cystine mismatch between feathers and other body tissues has received surpris-

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ingly little attention. All of the energy, amino acids, and other nutrients that are required for feather growth during the molt fast as well as other functions must be derived from catabolism of the penguin's tissues. Any significant mismatch between the essential amino acid profiles of feathers and of other tissue proteins will result in inefficient reutilization of amino acids in the production of the plumage and will require significantly greater storage of body protein before the onset of molt to meet the demands of feather synthesis. The inefficient use of tissue proteins in meeting the demands of feather synthesis would also require higher rates of catabolism of free amino acids because large quantities of free amino acids cannot be stored in the body. Consequently, much higher rates of nitrogen excretion would need to be sustained during the molt fast than if fat were catabolized to supply most of the energy required and amino acids were efficiently reutilized in protein synthesis (e.g., Ackerson and Blish 1926).

We recently reported that molting birds may rely on tissue glutathione (a cysteine-containing tripeptide) as a cysteine reservoir that may improve the efficiency with which tissue proteins are used in sustaining feather synthesis during the overnight fast (Murphy and King 1985, 1990). We hypothesize that this and similar storage mechanisms may be even more important to birds such as penguins that fast throughout much of the molt. Before undertaking studies of specialized amino acids storage by molting penguins, however, we thought it prudent to define the composition of their feathers (total protein, amino acids, ash) and evaluate the potential extent of the mismatch between feathers and other tissue proteins. The amino acid composition of the mixed proteins of adult contour feathers has been reported for a "penguin" (either *Pygoscelis adeliae* or *Aptenodytes forsteri,* or a blend of both: Brush and Wyld 1982) and roughly resembles the composition reported for feathers of other species. In this account we describe the chemical composition and the structure of feather parts in three species of penguins and discuss some of the metabolic implications of depending solely on body reserves to support keratin synthesis.

MATERIALS AND METHODS

We collected large samples of breast feathers from molting penguins, *P. adeliae* (Adelie), *P. papua* (Gentoo), and *P. antarctica* (Chinstrap), at Admiralty Bay, King George Island, in mid-February. To prepare specimens for chemical analysis and scanning electron microscopy (SEM) we washed subsamples of the feathers of each species in neutral detergent solution, 95% ethanol, and diethyl ether (Harrap and Woods 1964). For SEM we mounted trimmed sections of air-dried feathers on aluminum stubs, sputter-coated them with ca. 30 nm of gold (Technics, Hummer), and examined them at 20 kV in an ETEC U-1 autoscan scanning electron microscope.

For chemical analyses we first oven-dried samples of barbs and rachises from each species, then measured the nitrogen content of some by the micro-Kjeldahl method (Horwitz 1980) and the ash content of others by combustion in a muffle furnace (3 hr, 600°C). We measured the amino acid composition of hydrolysates of oven-dried samples by use of a Beckman model 121 MB ion-exchange chromatograph (Bioanalytical Laboratory, Washington State University). We hydrolyzed ca. 10-mg samples of each feather part in 6 *N* HCl for 20 hr, vacuum-dried the solutions, and redissolved the residues in sodium citrate buffer (pH 2.2). We measured the concentration of cyst(e)ine (reported herein as cystine/2) in parallel as cysteic acid after oxidation with performic acid (Schram et al. 1954).

RESULTS AND DISCUSSION

FEATHER STRUCTURE

As first reported by Chandler (1916), the rachises of penguin contour feathers are conspicuously broader than the rachises of the contour feathers of all other groups of birds. The penguin rachis (including calamus) dominates the mass of the contour feather, comprising 60 to 70% of the total mass (Table 1). In contrast, the rachis plus calamus comprises only about 20% of the mass of contour feathers in birds such as the White-crowned Sparrow, *Zonotrichia leucophrys gambelii* (King and Murphy 1987). We are confident that the very high rachis-to-barb mass ratio that we found in penguin feathers is not an artifact of differential wear of the barbs, since these feathers were almost indistinguishable by SEM from feathers newly grown by penguins of the same species at Hubbs Sea World Research Institute.

A very broad flat rachis appears to be a characteristic unique to penguin feathers. Stettenheim (1976) suggested that such a rachis and the spacing of barbs are adaptations for swimming

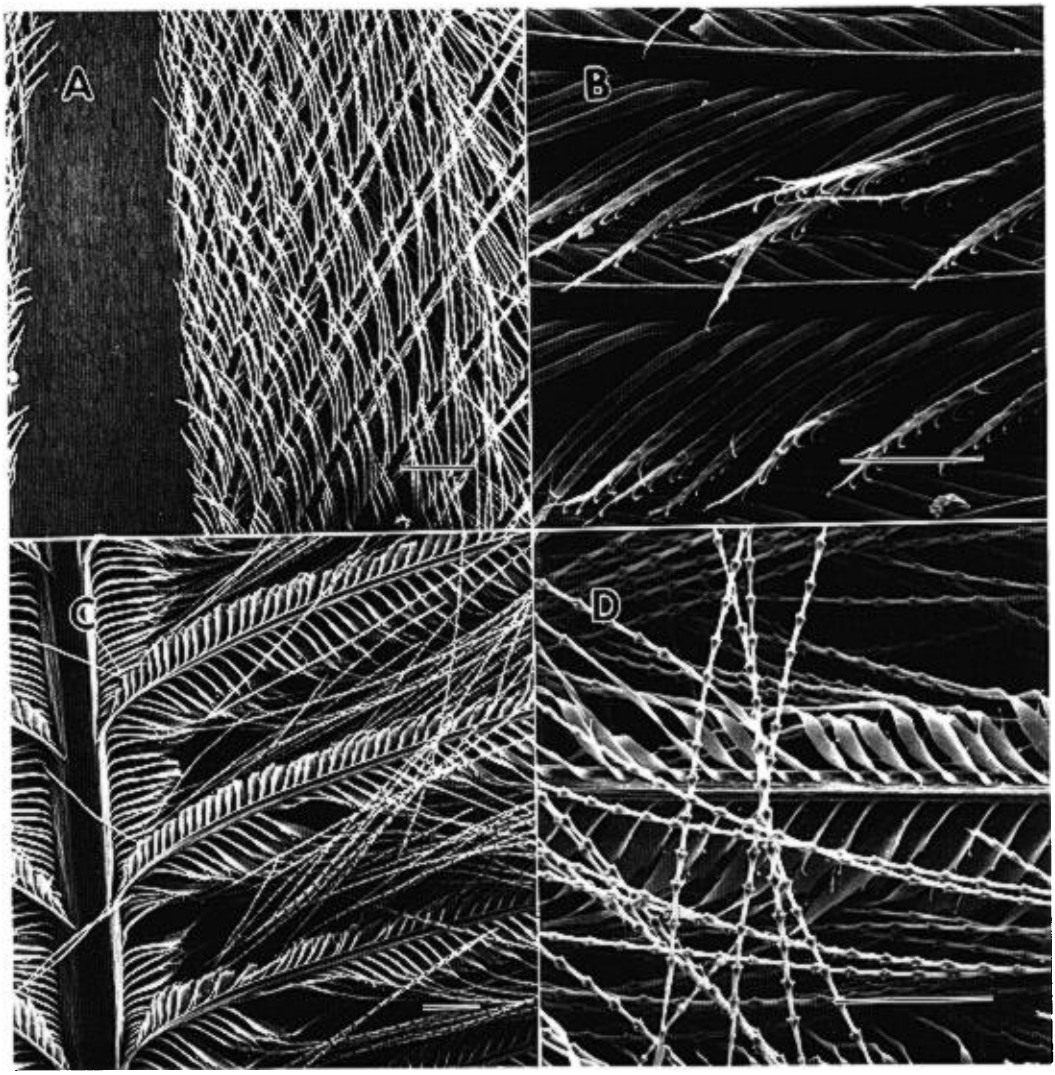

FIGURE 1. Scanning electron micrographs of the midsection of breast feathers of *Pygoscelis papua* (A, rachis and barbs; B, barbs and barbules) and *Zonotrichia leucophrys* (C, rachis and barbs; D, barbs and barbules). Scale bars are shown in lower right corner (A, bar = 200 μm; B, C, D, bar = 100 μm).

that improve water repellency and reduce drag. Similar adaptations are not apparent in other diving birds. Lowe (1933), however, argued that penguins "are the only truly aquatic group in the entire class" and that the unique features of penguin plumage are evidence of this distinction. Another advantage of the rigid structure of penguin feathers may be thermoregulatory. Stonehouse (1967) suggested that feather rigidity reduces convective heat loss.

In addition to the broad rachis of the penguin feather, microscopic differences may also con-

TABLE 1. Percentage of contour feather mass in barbs and rachises plus calami in *Pygoscelis* penguins.

Species	% rachises plus calami[1]	% barbs[2]
P. adeliae	60.1 (59.0–61.2)	39.9
P. antarctica	65.8 (65.4–66.6)	34.2
P. papua	69.9 (69.4–71.3)	30.1

[1] Mean of three samples of 250 mg each of clean contour feathers. Range is given in parentheses.
[2] Percentage calculated by difference.

TABLE 2. Mean percentage ± SE (n) nitrogen, water, and ash[1] content in clean feathers of three species of *Pygoscelis* penguins.

	Nitrogen content, % dry mass			Water content, % air-dried mass[2]
	P. adeliae	*P. antarctica*	*P. papua*	
Barbs	16.6 ± 0.041 (4)	16.5 ± 0.010 (3)	16.6 ± 0.006 (3)	9.26 ± 0.110 (6)
Rachis plus calamus	16.4 ± 0.024 (6)	16.4 ± 0.034 (6)	15.5 ± 0.048 (6)	8.00 ± 0.117 (6)

[1] Ash content was determined on triplicate 1-g samples of clean, dry whole feathers of each species. Average ash contents (±SE) equalled 0.72 ± 0.067, *P. adeliae*; 0.83 ± 0.035, *P. antarctica*; 2.61 ± 0.251, *P. papua*.
[2] Water content was nearly identical among samples of feather parts from the different species and data were combined for all species.

tribute to the high rachis-to-barb mass ratio (Fig. 1). The barbules of penguin contour feathers are pennaceous and able to interlock tightly, in contrast to the dense plumulaceous barbules of the contour feathers of many other species of birds (Lowe 1933, and Fig. 1). Moreover, interbarb intervals of the rachis are bare in penguin feathers, whereas at least in contour feathers of the White-crowned Sparrow, barbules arise in these intervals. In the next section we show that these pronounced structural differences in penguin feathers are reflected in only a few noteworthy compositional differences between penguin feathers and those of other birds.

FEATHER COMPOSITION: WATER, NITROGEN, AND ASH

Washed air-dried penguin breast feathers contained 8–10% water. The barbs, as might be expected from their greater surface/mass ratio, contained a significantly ($P < 0.001$ by t-test) larger proportion of water than the rachis, although the difference was small (Table 2). Unwashed air-dried feathers ($n = 6$) contained 10.0 ± 0.45% water, or ca. 1–2% more than the washed feathers. Washing thus obviates a small but appreciable error in estimating the true dry mass of the feathers.

The dried barbs of all three penguin species contained an average 16.6% nitrogen. Rachises of feathers from *P. adeliae* and *P. antarctica* likewise contained an average 16.4% nitrogen, but rachises from feathers of *P. papua* contained only 15.5% nitrogen (Table 2). The differing ash content of the dried feathers appears to account for the difference of nitrogen content between *P. papua* and its two congeners. The feathers of *P. adeliae* and *P. antarctica,* like those of White-crowned Sparrows, contain less than 1% ash by dry mass, whereas *P. papua* feathers contain 2.6% ash (Table 2). We suspect that these differing ash contents are related to the differing diets of these penguins. They all subsist primarily on one euphausiid species, but *P. papua* consumes significantly more fish (15% vs. <1%) than its congeners (Volkman et al. 1980). Minerals are sequestered in keratinous structures during their formation (e.g., Hanson and Jones 1976, Edwards and Smith 1984, Bortolotti and Barlow 1985). Apatite (calcium phosphate) occurs in various epidermal structures, including the calamus of goose feathers, and may be specifically deposited to contribute to the stiffness of the structures (Brown 1975). Why a greater deposition of minerals would occur in *P. papua* than in the other two species is unclear, but may be related to the mineral content of their diets.

The feathers of *P. papua* are distinguishable from those of the two other species not only by their proportionately greater ash content, but also by having a median basal streak of dense brown pigment. This mark is less common and shorter in feathers of *P. adeliae,* and is absent from feathers of *P. antarctica.* The presence of pigment would further reduce the percentage nitrogen content of dried rachises of *P. papua* as compared to the relatively unpigmented rachises of the other species. This is clearly illustrated by the differences between the nitrogen contents of the penguin feather parts and those of the heavily melanized feathers of White-crowned Sparrows (15.2% in homogenized sparrow plumage [15.1% in barbs and 15.5% in rachis]: Murphy and King 1982, King and Murphy 1987). Melanin contains ca. 7.2% nitrogen, which dilutes the nitrogen concentration per unit mass of a melanized feather. The nitrogen contents of the rachises of several domesticated species with white plumage range from 16.5 to 16.8% (Harrap and Woods 1967), much the same as the white penguin rachises.

FEATHER COMPOSITION: AMINO ACID PATTERN

To assess analytical precision we prepared duplicate samples of barbs from *P. adeliae* and *P. antarctica* and of rachises from *P. papua.* Pre-

TABLE 3. Amino-acid composition (μmoles/g dry mass) of the rachis plus calamus of contour feathers of *Pygoscelis* penguins.

Amino acid	*P. adeliae*	*P. antarctica*	*P. papua*
Essential[1]			
Arginine	328	321	326
Histidine	81	73	72
Lysine	44	45	40
Isoleucine	374	389	405
Leucine	986	923	924
Valine	724	737	737
Cystine/2	717	707	776
Methionine	73	68	73
Tyrosine	222	254	230
Phenylalanine	216	203	235
Threonine	392	409	436
Tryptophan[2]	ND	ND	ND
Nonessential			
Alanine	722	634	641
Aspartic acid	464	496	525
Glutamic acid	498	557	570
Glycine	1,477	1,386	1,405
Proline	1,035	986	1,002
Serine	933	785	792
NH_3 released[3]	689	698	659
% accounted for:			
Nitrogen	95	93	99
Dry mass[4]	93	91	93

[1] Including cystine and tyrosine which can be derived only from the essential amino acids methionine or phenylalanine, respectively.
[2] ND = not determined.
[3] Under conditions specified in the text.
[4] Calculated using dehydrated molecular weights of amino acids.

TABLE 4. Amino-acid composition (μmoles/g dry mass) of the barbs of contour feathers of *Pygoscelis* penguins.

Amino acid	*P. adeliae*	*P. antarctica*	*P. papua*
Essential[1]			
Arginine	337	335	339
Histidine	78	33	30
Lysine	78	80	75
Isoleucine	424	436	431
Leucine	727	729	741
Valine	839	860	845
Cystine/2	782	878	786
Methionine	103	112	101
Tyrosine	243	257	215
Phenylalanine	203	178	199
Threonine	437	452	452
Tryptophan[2]	ND	ND	ND
Nonessential			
Alanine	499	503	506
Aspartic acid	628	630	615
Glutamic acid	685	709	684
Glycine	1,155	1,096	1,109
Proline	1,044	1,074	1,046
Serine	703	716	727
NH_3 released[3]	858	864	873
% accounted for:			
Nitrogen	93	94	92
Dry mass[4]	93	95	92

[1] Including cystine and tyrosine which can be derived only from the essential amino acids methionine or phenylalanine, respectively.
[2] ND = not determined.
[3] Under conditions specified in the text.
[4] Calculated using dehydrated molecular weights of amino acids.

cision was very good, as judged by the close agreement between samples. We used norleucine as an internal standard for all analyses. The mean absolute differences between duplicate samples were 1.5% in barbs of *P. adeliae,* 3.3% in barbs of *P. antarctica,* and 2.2% in rachises of *P. papua.* The maximum differences between individual amino acids within a sample were well below the acceptable limits (ca. 8%) of sampling error and analytical precision described by Williams (1981) for the analytical methods that we used.

The amino acid analyses accounted for an average of 94% of the dry mass of the penguin barbs and rachises, ranging from 91% to 95% in the six samples (Tables 3, 4). This exceeds the dry mass recovery (82–86%) obtained by identical methods of analysis in White-crowned Sparrow feathers (Murphy and King 1982, King and Murphy 1987). An unknown fraction of the 10% difference between penguins and sparrows results from the heavy pigmentation of the sparrow feathers, as already mentioned. We do not know the proportional mass of these pigments in sparrows, but it has been estimated in other species that pigments constitute at least 3–5% of total feather mass (Nicholaus et al. 1964).

Amino acids and NH_3 accounted for an average of 94.6% of the nitrogen in penguin feathers (range = 92.5–99.5%), which is about the same as found in White-crowned Sparrow plumage (93–97%: King and Murphy 1987), and in several species of domestic fowl, a gull (*Larus*), and the Emu (*Dromaius novaehollandiae*) (90–101%: Harrap and Woods 1967).

The amino acid profiles of both rachises (Table 3) and barbs (Table 4) were essentially indistinguishable among the three species of penguins. The coefficients of determination were >0.99 for all comparisons within parts (barbs or rachis including calamus) between species. Parts differed more within species than between species, with $r^2 = 0.87$, 0.92, and 0.89 in barb vs. rachis comparisons in *P. adeliae, P. papua,* and *P. antarctica,* respectively. Brush (1978) also noted in a

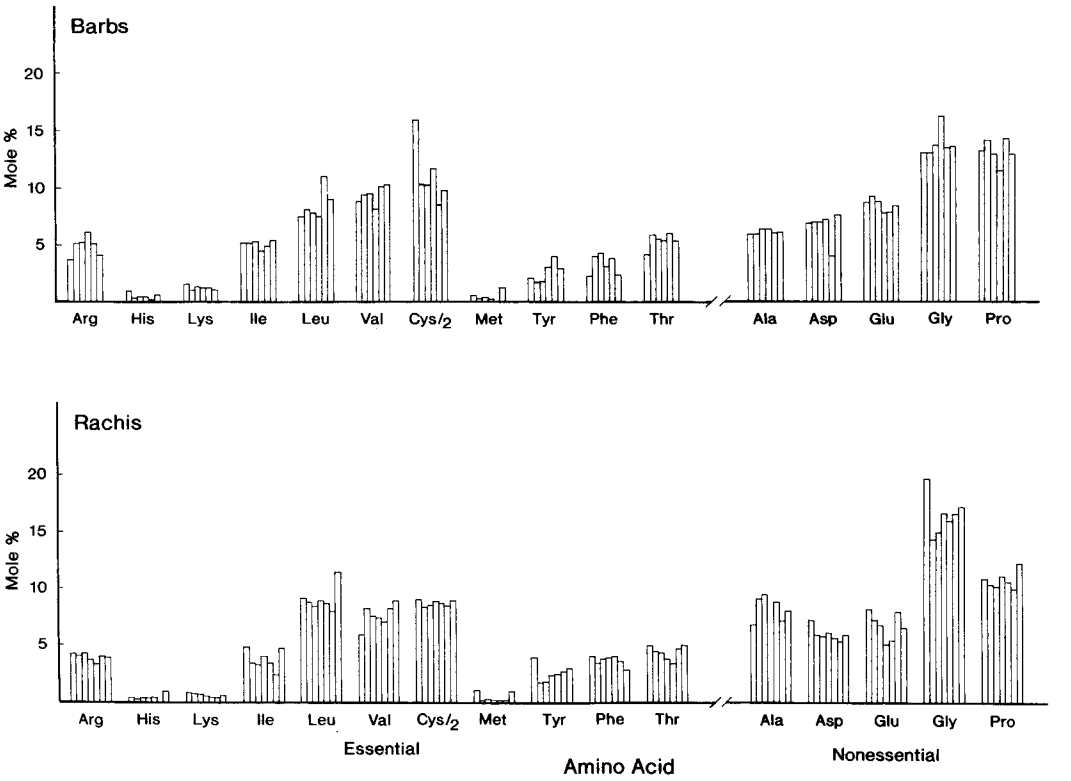

FIGURE 2. Amino-acid profiles of feather barbs and rachises of several species of birds. Species included in the plot of barbs are (right to left) White-crowned Sparrow (King and Murphy 1987), chicken, turkey, goose, Emu (Harrap and Woods 1967), and mean pygoscelid penguins (this report). Birds included in the plot of rachises are (right to left) White-crowned Sparrow (Murphy and King 1987), chicken, turkey, goose, duck, gull (Harrap and Woods 1967), and mean pygoscelid penguins (this report). Data are reported as mole % excluding tryptophan, which was not determined, and serine, which is particularly susceptible to destruction during acid hydrolysis (see Murphy and King 1986).

much larger variety of species that amino acid profiles differed more between parts within species than among homologous parts across species.

TAXONOMIC COMPARISONS OF THE AMINO ACID COMPOSITION OF FEATHER PARTS

The amino acid profiles of penguin feather parts are remarkably similar to those of other species of birds representing six different orders and varied lifestyles (Fig. 2; see also Brush and Wyld 1982). This similarity illustrates the genetically conservative status of the feather keratins. Two notable differences in the amino-acid profiles among these species are: (1) penguin feather parts tend to contain slightly more of the branched-chain amino acids, particularly leucine, than in the other species; and (2) White-crowned Sparrow feather barbs, but not rachises, contain substantially more cystine/2 than barbs of any of the other species in Figure 2. Because of this higher concentration of cystine/2 in barbs, a large shift in the apportionment of feather mass from barb to rachis in White-crowned Sparrows would result in a considerable decrease in the cystine requirement for feather synthesis (the cystine/2 content of rachis is only 60% that of barbs in this species). This effect is not nearly as great in the penguins, but some incidental saving of cystine/2 does result from the predominance of the rachis in the morphology of penguin feathers. The rachis of penguin feathers contains 10% less cystine/2 than the barbs. The difference in cystine/2 content of barbs and rachis of the other species described is less than in the White-crowned Sparrow or in the penguins. However, in the Emu, in spite of the relatively low cystine/

2 contents of its feathers, the difference in cystine/2 contents between calamus and barbs is nearly 30% (calamus less than barbs).

COMPARISON OF FEATHER COMPOSITION AND TISSUE PROTEIN COMPOSITION

The foregoing analysis suggests that pygoscelid penguins are subject to the same mismatch of amino acids between feathers and other tissue proteins as occurs in other birds (Fig. 3). The first limiting amino acid in the formation of feathers from mixed carcass proteins or from mixed muscle proteins is cystine/2, followed by valine and leucine. The remaining essential amino acids are all more concentrated in mixed tissue proteins than in feathers. We estimate that synthesis of 1 g of feather protein by penguins requires an amount of cysteine (762 μmoles of cystine/2) equal to that contained in 7.8 g of mixed tissue protein or 8 g of muscle protein. This estimate is based on the amino-acid composition of the mixed proteins of integument-free gosling carcasses (98 μmoles of cystine/2 and 137 μmoles of methionine per gram: Nitsan et al. 1981) and of muscle protein of the chicken and turkey (95 μmoles of cystine/2 and 198 μmoles of methionine per gram: Scott 1959). Cystine/2 is also available by synthesis from methionine with nearly 100% molar efficiency (Graber and Baker 1971). When this source is included, we calculate that the amount of total SAA needed by penguins to produce 1 g of feather protein roughly equals the amount of SAA contained in 2.9 g of muscle protein or 3.6 g of mixed tissue protein. In the absence of any cysteine reserve, such as glutathione, a pygoscelid penguin would have to store an amount of tissue protein not just equal to, but exceeding 2.9- to 3.6-fold the mass of the plumage to be synthesized during the molt fast. At best, 95% of the SAA available from stored protein would be reutilized (Waterlow et al. 1978) for plumage synthesis. Moreover, ordinary metabolic requirements that continue during the molt fast also depend on the reutilization of stored SAA (e.g., sulfur donors, methyl donors, synthesis of taurine and of proteins other than keratin). The inefficiency of reutilization and the diversion of SAA to processes other than molt combine to inflate the need for stored protein to an unknown extent beyond the minimum required by plumage regeneration.

The foregoing analysis concerns the first limiting amino acid in plumage synthesis. A similar

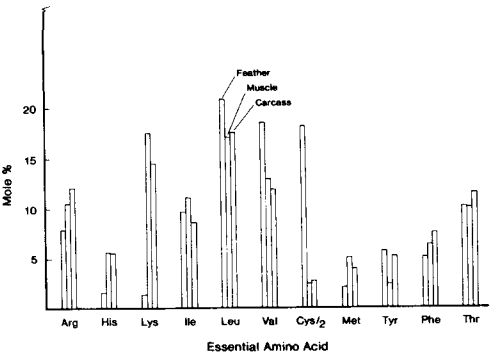

FIGURE 3. Essential amino-acid profile of whole feathers of pygoscelid penguins (this report), of mixed muscle proteins of chickens and turkeys (Scott 1959), and of mixed carcass proteins (excluding integument) of growing goslings (Nitsan et al. 1981). Data are presented as mole % of total essential amino acids plus tyr and cys/2. The amino acids plotted represent 40–45% the total μmoles of amino acids and 45–50% of the total mass in the mixed proteins indicated. The use of amino-acid profiles from these domesticated species to represent penguin proteins is justified by the close similarity of amino acid composition of body proteins among vertebrate species (Maynard et al. 1979).

analysis of the amount of stored protein needed to supply the second limiting amino acid (valine, with 773 μmoles/g feather protein, 510 μmoles/g muscle protein, and 424 μmoles/g mixed tissue protein) and the third limiting amino acid (leucine, with 870 μmoles/g feather protein, 674 μmoles/g muscle protein, and 637 μmoles/g mixed tissue protein) indicates that as little as 1.3–1.8 g of tissue protein would contain an amount of these amino acids equal to that in 1 g of feather protein. Hence, only about half as much protein needs to be stored to satisfy the requirements for valine and leucine as compared with the SAA. This illustrates the role of SAA availability as the dominant bottleneck in the synthesis of keratin during the molt fast.

Penguins apparently circumvent some of the metabolic inefficiencies attending plumage synthesis during the molt fast by synthesizing as much as one-third of the plumage before coming ashore, presumably while still feeding at sea, and before beginning to shed the old plumage (Lowe 1933, Brown 1986). Later, during the molt fast, the use of supplemental cysteine stored previously in a donor compound such as glutathione (Murphy and King 1985, in press) is a mechanism by which penguins could nearly double the

efficiency with which they use tissue protein in feather synthesis. We believe that this possibility merits further investigation.

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