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Energetics and Nutrition of Molt

Mary E. Murphy

The most salient feature of the class Aves is the ubiquity of feathers. These structures play vital roles in thermoregulation, protection, communication, and locomotion in birds (Stettenheim 1976). The maintenance of the integrity of its feather coat, or plumage, is essential to a bird's survival. The periodic replacement of all or parts of the plumage is known as molt. Molt undoubtedly requires a wide array of adjustments in the physiology, energetics, and nutrition of birds. What is known about these adjustments is the focus of this chapter. Different groups of birds have evolved different schemes for molting. Variation in patterns and timing of molt among groups of birds have been reviewed by others (Stresemann and Stresemann 1966; Palmer 1972; Payne 1972; King 1974; Boere 1976; Hahn et al. 1992) and are discussed here only briefly.

APPARENT NUTRITIONAL REQUIREMENTS FOR MOLT

The apparent, or theoretical minimum, requirements of a productive process can be derived from a knowledge of the composition and rate of growth of the product. The actual requirements also include energy and nutrients lost owing to inefficiency of absorbing, processing, and utilizing nutrients, as well as the metabolic costs (above the maintenance level) involved in establishing a permissive background for growth.

Molted Structures and Their Masses

All birds regenerate their entire corneous (keratinized) surface repeatedly throughout their lives. A complete molt involves at least replacement of all of the

C. Carey (ed.), *Avian Energetics and Nutritional Ecology*
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feathers and the production and sloughing of the ephemeral, protective feather sheaths. In some species, sloughing and replacement of the whole stratum corneum may coincide with feather replacement (King and Murphy 1990). However, replacement of the stratum corneum is probably a continuous process (Spearman and Hardy 1985), even if the rate of its replacement varies annually. The sloughing and replacement of the horny coverings of the beak (rhamphotheca) and the legs and feet (podotheca) may coincide with feather replacement in some species, or occur earlier or later in other species (for review see King and Murphy 1990).

In *Zonotrichia leucophrys gambelii,* the relative ratio of feathers to sheath to other corneous structures regenerated during the complete, prebasic molt is 20:4:1 (Table 6.1). Comparable data are not available for other species. The relationship between mass of feathers and sheaths produced during molt may be constant across species. The main purpose of the feather sheath is to protect the pulp region of the growing feather, especially from desiccation. Lillie (1940) describes a predictable relationship between growth and length of the pulp and that of the feather.

The plumages (y) of birds, excluding the ephemeral sheaths, amount to about 4% (e.g., *Eudyptula*) to 12% (e.g., *Parus*) of body mass (W in g) and can be roughly approximated by the equation, $y = 0.09W^{0.95}$ (i.e., ca. 6% body mass; Turček 1966). Apart from genotypic differences, some of the variation in the relationship between plumage and body mass among species undoubtedly results from annual variation in body mass in many birds that makes it difficult to determine basal mass and from the continual net loss and wearing of feathers that can occur between molts (e.g. Markus 1965; Dawson and Carey 1976; Middleton 1986). Moreover, plumages as well as corresponding individual feathers can vary in mass between seasons in some species (Middleton 1986). Thus, even within an individual bird,

TABLE 6.1 Air-Dried Mass of Corneous Structures of *Zonotrichia leucophrys*

Structure	Mass (g)	% Plumage Mass
Plumage	2.08	—
Body feathers	1.61	77.4
Remiges	0.31	14.9
Rectrices	0.16	7.7
Feather sheaths	0.40	19.2
Stratum corneum	0.09	4.3
Podotheca (both legs)	0.02	0.9
Rhamphotheca	?	?

Note: For additional details, see Murphy and King (1984a; 1986a) and King and Murphy (1990).