ESTIMATES OF THE MASS OF STRUCTURES OTHER THAN PLUMAGE PRODUCED DURING MOLT BY WHITE-CROWNED SPARROWS[1]

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Abstract. Analysis of the caloric or nutritional demands of molt requires a thorough inventory of the mass and composition of all molted structures and of the ephemeral nonmolted structures (e.g., feather pulp) that accompany the process. Only plumage mass and composition are adequately known in a selection of species. We reported previously that the air-dried plumage mass of a 27-g White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) is about 2,000 mg at the end of the postnuptial (PN) molt, during which about 400 mg of feather sheaths were grown and shed. In this report we show that the stratum corneum (air-dried mass = 88 mg) of captive *Z. l. gambelii* is totally shed and replaced during the PN molt, and that the podotheca (19 mg, both legs) is molted about 10 weeks later, in November. The rhamphotheca is not shed during feather molt, but appears to be renewed continuously in response to wear of the tomia. It is unlikely that the molt of the podotheca is delayed because of nutritional stringency during the PN molt, since its mass is only about 1% of the combined mass of feathers, sheaths, and stratum corneum. Very little is known in other species about the renovation of corneous structures other than feathers. It is thought that skin, beak, and claws grow continuously in response to wear, and that the skin also molts totally during feather molt. In some species, claws and parts of the beak may also be shed episodically during or near the time of feather molt. The podotheca is probably shed annually in all species, often during feather molt but sometimes earlier or later.

Key words: Molt; stratum corneum; claws; beak; podotheca; White-crowned Sparrow; Zonotrichia leucophrys.

INTRODUCTION

Avian molt entails the synthesis and deposition of large amounts of keratin in the forms of feathers and other corneous parts of the integument. An accurate analysis of the caloric and nutritional costs of molt requires a thorough inventory of the dry mass and chemical composition of these parts and of the ephemeral structures, such as feather sheaths, pulp, and external pulp caps, that play a role in the renovation of the integument. Total plumage mass can be estimated roughly from allometric equations (Brody and Campbell 1938, Turček 1966), but there are almost no data available on the mass or composition of other molted or molt-related structures. In an earlier report (Murphy and King 1986) we estimated that feather sheaths produced and shed by White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) during the postnuptial molt weighed 380–420 mg—a mass equivalent to at least 18–20% of the mass of the new plumage,

and hence not negligible. Nothing has been reported heretofore in this or any other species about the extent to which the molts of other corneous structures such as the stratum corneum of the skin and the horny coverings of the beak (rhamphotheca) and the legs and feet (podotheca) add to the costs of production and to net nitrogen retention. In this report we undertake to estimate the relative importance of some of these structures in compiling the caloric or material costs of molt.

MATERIAL AND METHODS

We weighed (±0.002 mg) air-dried samples of stratum corneum (henceforth "skin") shed by *Z. l. gambelii* engaged in normal postnuptial molt. Samples large enough to permit accurate measurement of both mass and area were infrequent and could be obtained only by stripping loose patches of skin from the ventral apterium. We measured the area of each sample by dividing the mass of an exact facsimile cut from high-quality graph paper (the same sheet for all samples) by the mass of 1.00 cm² of the same paper.

TABLE 1. Measurements of the mass and surface area of samples of molted stratum corneum from the ventral apterium of White-crowned Sparrows.

Sample rank[1]	Sample no.[2]	Stratum corneum		
		Mass (mg)	Area (cm²)	Mass/area (mg/cm²)
1	2	1.210	1.094	1.106
2	5	0.694	0.651	1.066
3	6	0.688	0.587	1.172
4	4	0.672	0.594	1.131
5	1	0.520	0.524	0.992
6	3	0.460	0.361	1.274
$\bar{x}$		0.707	0.635	1.124
SE		0.1081	0.1004	0.0392

[1] Ranked in the order of decreasing mass.
[2] Samples 1–3 = batch 1, samples 4–6 = batch 2 (see text).

We made the facsimiles by carefully smoothing a sample of skin onto graph paper with a small brush and gently pressing it flat with a square of parafilm, to which skin does not stick. We cut the sample's exact shape from the paper with the edge of a 24-ga hypodermic needle used as a small knife. To help assess analytical precision we treated the samples ($n = 6$ birds) in two batches of three, each with its own 1-cm² paper standard.

The podothecae are typically shed as fragments, although sometimes we found almost complete tubular sections of tibiotarsal thecae when cleaning metabolism pans. To obtain intact thecae we resorted to dissection from dead specimens. The tibiotarsal theca from its junction with the skin of the femur to the proximal edge of the first scute of the third toe was readily parted from underlying tissue by first making a midline cut along the back of the tibiotarsus, followed by annular cuts at the two ends. Soaking the amputated leg in hot water for a few minutes made the dissection easier and minimized adherent tissue (Lucas and Stettenheim 1972, p. 597). The specimens (both legs from three birds = 6) were air-dried to constant mass (±0.05 mg).

RESULTS AND DISCUSSION

WHITE-CROWNED SPARROWS

Skin. The mean specific mass (±SE) of air-dried stratum corneum was 1.12 ± 0.039 mg/cm² (Table 1). Analytical precision and repeatability were adequate between two batches of samples. The standard square of graph paper weighed 8.31 mg/cm² in batch 1 and 8.52 mg/cm² in batch 2. Ranking the samples according to surface area did not reveal any systematic bias associated with their size (Table 1).

The entire skin surface "desquamates" during feather molt in domestic pigeons (Voitkevitch 1966, p. 56) and probably in all species of birds (Spearman 1966, p. 73). We have found loose stratum corneum in all major apteria in *Z. l. gambelii* during prenuptial as well as postnuptial molt, which indicates that the skin surface is rejuvenated completely in this species. The total skin-surface area, excluding the beak and unfeathered legs and feet, of an average (27.3 g) *Z. l. gambelii* is about 80.0 cm² (Walsberg and King 1978, table 1), divided between apteria and pterylae. Part of the surface area of the pterylae is occupied by feather shafts, but proves to be very small. To illustrate: the maximum diameter of the calamus of *Z. l. gambelii* contour feathers is about 0.2 mm, which corresponds to a cross-sectional area of about 3.14×10^{-4} cm². This species bears an average of about 3,448 contour feathers (Kronberg 1981). The net *maximum* skin area (the diameter of many calami is less than 0.2 mm) not occupied by feather shafts is therefore about $80.0 - (3,448 \times [3.14 \times 10^{-4}]) = 78.9$ cm², or 98.6% of the total area. The total mass of stratum corneum shed (and presumably regenerated), assuming that the area-specific mass of samples from the ventral apterium adequately represents the entire body, is therefore $78.9 \times 1.12 = 88.4$ mg. This equals about 4.0% of the air-dried plumage mass, and so is a minor element in evaluating the costs of molt, although not necessarily negligible.

Legs and feet. The podothecae of captive *Z. l. gambelii* are apparently totally shed once a year about 3 months after the end of the postnuptial molt. We have found large fragments of shed podothecae (sometimes almost complete tubes sloughed from the tibiotarsus) in metabolism cages only in November, and never during the postnuptial feather molt itself. We concede that very small thecal fragments might go unnoticed in metabolism pans at other times of the year, and that renovation of the podothecae might be continuous; but the peak of sloughing in November is clear-cut, and suggests a total molt of the legs and feet at that time. The subject requires more investigation.

The reason for the apparent temporal offset between feather and skin molt and podothecal molt is probably not related to nutritional costs in the production of this structure. We found that

the dissected theca of the tibiotarsus in *Z. l. gambelii* weighed (air dry) about 8.9 mg, had an area of 2.9 cm^2, and a specific mass of about 3.0 mg/cm^2 (Table 2). By modeling the legs and toes of this bird as a set of right cylinders and elliptical cylinders, Walsberg and King (1978) estimated that the total surface area of the podothecae of both legs averages 6.3 cm^2. If the average specific mass is the same as that of the tibiotarsal theca, then the mass of the podothecae (both legs) is about 3.0 × 6.3 = 18.9 mg. This may be an underestimate, since it seems probable that the theca of the toes, and especially the pads, may be thicker than that of the tibiotarsus. From this analysis, it appears that the dry mass produced in the renewal of the podotheca amounts to less than 1% of the combined mass of feathers (ca. 2,000 mg), sheaths (ca. 400 mg), and stratum corneum (ca. 88 mg) produced during molt. The apparent delay in the molt of the podotheca by *Z. l. gambelii* until after the end of feather molt must result from something other than nutritional stringency.

Beak. The White-crowned Sparrow's rhamphotheca, like that of other birds, grows continuously in proportion to abrasion of the tomia, and perhaps responds in size to seasonal stimuli (Morton and Morton 1987). This growth is budgeted to maintenance, not to molt or special production. We have no evidence that the growth of the rhamphotheca is accelerated during the postnuptial molt in *Z. l. gambelii* (but see below for discussion of other species). On the contrary, the length of the bill in free-living Mountain White-crowned Sparrows (*Z. l. oriantha*) recedes from its midsummer maximum before the onset of the postnuptial molt (Morton and Morton 1987).

Net nitrogen retention. During a 54-day postnuptial molt *Z. l. gambelii* retains, as measured by nitrogen balance (Murphy and King 1984), about 620 mg of the nitrogen that it ingests in protein. We have previously noted (Murphy and King 1986) that the synthesis of feathers (324 mg N) and sheaths (61 mg N) accounts for only 385 mg of this total. Part of the stimulus for the present investigation was to learn if other molted structures accounted for a significant part of the apparent deficit. As could be inferred from the relative masses reported above, stratum corneum and podothecae do not help much to close the gap. If we assume that these structures have the same nitrogen content as feather sheaths

TABLE 2. Measurements of tibiotarsal thecae dissected from White-crowned Sparrows.

Bird and leg	Diameter[1] (mm) a	Diameter[1] (mm) b	Length (mm)	Area[2] (cm^2)	Mass (mg)	Mass/ area (mg/cm^2)
Bird 1-1	2.3	1.3	23.2	2.72	8.49	3.12
1-2	2.4	1.3	23.0	2.79	8.64	3.10
Bird 2-1	2.2	1.5	24.6	2.91	9.12	3.13
2-2	2.4	1.5	24.8	3.12	9.05	2.90
Bird 3-1	2.4	1.6	24.3	3.11	9.19	2.95
3-2	2.4	1.4	24.3	3.00	8.99	3.00
$\bar{x}$				2.94	8.91	3.03
SE				0.067	0.115	0.039

[1] Major and minor axes.
[2] Area (cm^2) = $0.02\pi h\sqrt{[(a^2 + b^2)/2]}$, where h = length of the tibiotarsal theca.

(15.2%), then it follows that deposition of the stratum corneum accounts for 14 mg N during molt and the podothecae for 3 mg N. The sum of feathers, sheaths, skin, and podothecae is 402 mg N, leaving 218 mg N still not accounted for. This apparent deficit results from noncloacal losses of nitrogen that eluded our analysis, or from retention of nitrogen in N-containing compounds other than those that we have analyzed, or both. We have reviewed elsewhere (Murphy and King 1984, 1986) some major structures and processes (e.g., synthesis and resorption of feather pulp, expansion and retraction of blood volume, net gain in carcass protein) that potentially will help balance the net nitrogen equation. Progress beyond our present state of knowledge about the nutrition and metabolism of molting birds will depend on further analysis of these processes.

OTHER BIRDS

In an attempt to learn the degree to which we might generalize from our data on *Z. l. gambelii* we consulted all the literature references that we could find about the timing and extent of molt in integumentary structures other than feathers. Such information is unexpectedly sparse, as illustrated by the brief mention (or none) of these subjects by authorities such as Stresemann (1927–1934), Mayaud (1950), Berndt and Meise (1962), Spearman and Hardy (1985), Campbell and Lack (1985), Sawyer et al. (1986), and so on. To spare others a repetition of this search we briefly summarize here the fragments of information that we have unearthed so far on a handful of species.

As generalizations, the avian rhamphotheca and claws (Mayaud 1950, Rawles 1960) and the

stratum corneum (Spearman and Hardy 1985) are thought to be renewed continuously, although these structures may also be molted episodically in some species (see below). We have already cited evidence that the stratum corneum is sloughed and replaced during feather molt in at least some species of birds. The molt of other corneous structures may coincide with feather molt in some species, or occur earlier or later in other species. Tetraonids are reported to shed their claws once a year during the summer feather molt (Stejneger 1884, Committee of Inquiry on Grouse Diseases 1911 [plate XIII], Mayaud 1950, Evans 1985). Mayaud (1950, p. 9) also stated that the rhamphotheca in *Tetrao* and allied genera is shed in a single step ("d'un seul coup") after the end of the breeding season, and that a regular molt of the leg scales occurs in certain tetraonids, and perhaps also in small passerines, in summer (p. 13). Captive Little Owls (*Athene noctua*) have been observed to shed the tip of the upper beak ("by then grown quite long") in August or September (Tavistock 1917).

Spearman (1966, p. 73) generalized that the replacement of the podotheca probably occurs during the annual feather molt. A case cited by Evans (1985) in the Song Thrush (*Turdus philomelos*) is consistent with this suggestion. In the American Coot (*Fulica americana*), however, molt of the podotheca may precede feather molt by as much as 6 weeks (Gullion 1953). In captive *Z. l. gambelii* molting on a normal schedule the podotheca tends to be shed, as we have already noted, about 10 weeks or more after the end of the feather molt. The postnuptial shedding of the bill-plates and eye-ring ornaments in the Atlantic Puffin (*Fratercula arctica*) coincides with feather molt in the bird's head and neck, but occurs much earlier than the feather molt of the body, wings, and tail (Bureau 1877, Harris 1984). The carpal spurs of the Spurwinged Goose (*Plecopterus gambensis*) are shed near the end of the annual wing molt (Zaloumis 1982).

In summary, it seems likely from the available evidence that the stratum corneum, claws, and tomia of the rhamphotheca are renewed continuously in proportion to wear. It appears that the stratum corneum is also totally replaced during feather molt, as are the claws and parts of the rhamphotheca in at least some species. The podotheca is probably molted totally once a year, in many if not all species, following the breeding season but not necessarily coincident with the

feather molt. The repeated equivocations in the foregoing summary emphasize how little we know, on a comparative scale, about the physiology and dynamics of molt apart from the renewal of the plumage. Progress toward a reliable analysis of the molt's potential as a nutritional or caloric bottleneck in the avian annual cycle could be greatly accelerated by filling in some of the gaps in knowledge that we have illuminated in this report. Opportunities are wide open for very significant investigations of a strangely neglected subject.

ACKNOWLEDGMENTS

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