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PROTEIN COSTS OF THE PREBASIC MOLT OF FEMALE MALLARDS¹

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The nutritional requirements and physiological mechanisms of avian molt and the relationship of molt to other ecological requirements in birds are poorly understood. Relative to other nutritionally costly events in the annual cycle (e.g., reproduction and migration), the efficiency of feather synthesis is extremely low (King 1981, Murphy and King 1984a). Gavrilov and Dolnik (1974) suggested that this inefficiency was caused by an aminostatic regulation of food intake which allows acquisition of sufficient cysteine and cystine for construction of feather keratins. Recent investigations failed to confirm this "aminostatic hypothesis," however, and instead suggested that overall nitrogen retention (of the correct amino acid spectrum), not specific sulfur amino acid (SAA) concentrations, may be a more important constraint on feather synthesis, and that both protein and SAA requirements can be met through dietary intake without depleting tissue proteins (Murphy and King 1984a, 1984b, 1984c, 1985). Also, studies of wild Eurasian Bullfinches (*Pyrrhula pyrrhula*) (Newton 1968), the Canada Goose (*Branta canadensis*) (Raveling 1979, Mainguy and Thomas 1985), the Lesser Snow Goose (*Chen caerulescens*) (Ankney 1979), Brant (*Branta bernicla*) (Ankney 1984), and Mallard (*Anas platyrhynchos*) (Heitmeyer 1985) indicate that molting birds typically obtain protein and SAA required for feather synthesis from food.

The actual protein intake needed to synthesize feathers is not known for any bird in the wild, and only White-crowned Sparrows (*Zonotrichia leucophrys*) have been intensively studied in the laboratory in an attempt to calculate protein costs (Murphy and King 1982, 1984a, 1984b). Studying molt with captive birds has been hampered, however, because captive birds often

do not undergo a typical molt if (1) photoperiod, temperature, food quantity and quality, and social settings are artificial, (2) birds are unnaturally constrained, or (3) locations are distant from the site where molt would occur naturally (West 1968, Blackmore 1969, King 1974, Chilgren 1978).

In contrast to laboratory investigations, studying the cost of molt in the wild is hampered because variables affecting the bird and its environment are not controlled, and the intake and output of nutrients are not measured. Despite these problems bioenergetic costs can be accurately estimated from birds collected in the wild if sufficient data exist on the pattern, timing, and duration of synthesis, and composition of the synthesized product (e.g., estimates of bioenergetic costs of reproduction, Ricklefs 1974, Drobney 1980). Herein, I estimate the protein cost of the prebasic molt of adult female Mallards in late winter using birds collected in the wild.

METHODS

Adult female Mallards were collected from January through March 1981 and October through March 1981 to 1982 and 1982 to 1983 in the Mingo Basin of southeastern Missouri ($n = 175$), and during March 1981 and 1983 at the Ted Shanks Wildlife Management Area in northeastern Missouri ($n = 8$). Similar numbers of Mallards were collected each month (Heitmeyer 1987). Collected birds represented all stages (i.e., 0 to 100%) of molt completion and were representative of the population present in the Mingo Basin (Heitmeyer 1985, in press). All feathers were plucked from each bird and the percentage completion of the prebasic molt in each of 18 feather areas determined as described in Heitmeyer (1987). The mass (g, dry weight) of all feathers replaced (via the prebasic molt) on each bird when collected was calculated by multiplying the percentage of each feather area that had molted into the basic plumage by the dry mass of the completely replaced basic plumage of each area and summing all areas. The dry mass of the basic plumage was determined by plucking and drying (80°C to a constant weight) all feathers from the 18 feather areas, plus the wing, from six adult female Mallards that had completed the pre-

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TABLE 1. Mean dry mass (g) and percentage of feathers on different areas of adult female Mallards in basic plumage ($n = 6$).

Feather area	$\bar{x} \pm SE$	% Dry mass
Crown	0.81 \pm 0.01	1.11
Facial	0.85 \pm 0.01	1.17
Chin	0.23 \pm 0.01	0.32
Neck	8.03 \pm 0.30	11.05
Upper back	3.09 \pm 0.15	4.25
Lower back	3.67 \pm 0.14	5.05
Rump	4.61 \pm 0.16	6.35
Upper tail coverts	0.94 \pm 0.04	1.29
Tail	2.31 \pm 0.32	3.18
Lower tail coverts	1.47 \pm 0.04	2.02
Chest-center	4.02 \pm 0.21	5.53
Chest-side	4.02 \pm 0.16	5.53
Side	4.29 \pm 0.22	5.90
Flank	2.94 \pm 0.17	4.04
Belly	5.15 \pm 0.37	7.09
Tertials	1.93 \pm 0.07	2.66
Scapulars	3.84 \pm 0.16	5.29
Greater coverts	1.45 \pm 0.03	1.99
Wing ^a	19.02 \pm 0.47	26.18
Total	72.67 \pm 0.30	100.00

^a Primaries, secondaries, primary and secondary coverts, tertial coverts, wing lining, axillaries.

basic molt. The mean mass of feathers replaced during each decile of percentage molt completion was calculated by subtracting the mean mass of feathers replaced at the end (last 10%) of each decile from the cumulative mean mass of feathers replaced at the end of the succeeding decile.

The protein costs of the entire and each decile of the prebasic molt were calculated by multiplying the weight of feathers replaced by the protein content of feathers (86.2% of dry body feather mass, Wielicki 1987) times the overall efficiency of converting dietary protein into feathers (55 to 69%, Scott et al. 1976:80–81, Murphy and King 1984b:331). This overall efficiency is normally calculated by multiplying the efficiency of digesting dietary protein (digestive efficiency) by the efficiency of converting digested protein into feather protein (conversion efficiency). However, the efficiency of converting digested protein into feather protein is largely unknown for birds, (see Fisher 1980:268; Murphy and King 1984a, 1984b, 1986), because protein costs associated with, and in addition to, amounts deposited in the final complement of feathers are not known. These additional costs include (1) growth of more feathers than the final number and weight (i.e., some feathers of wild birds are undoubtedly lost and regrown more than once during a molt), (2) regeneration of epidermal structures other than feathers (e.g., corneous of skin, podotheca, elements of the rhamphotheca) (Murphy and King 1986), and (3) constituents of the feather pulp (Murphy and King 1984b). Since the conversion efficiency is unknown for Mallards, I used 55% overall efficiency (this efficiency seems most realistic for nonpasserines, Scott et al. 1976) to

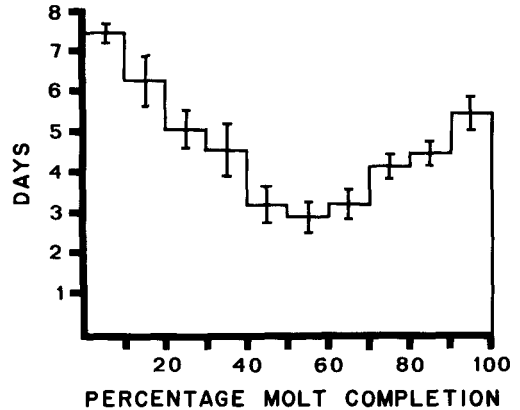


FIGURE 1. Mean number of days required to complete each decile of the prebasic molt of adult female Mallards collected in Missouri, 1981 to 1983. Vertical bars indicate standard errors.

estimate protein costs. While future studies of conversion efficiency in Mallards may correct the estimation of final protein costs, my attempt to demonstrate patterns and significance of protein requirements for the prebasic molt of female Mallards should not be altered.

Protein costs/day were determined by dividing the protein cost of each decile of molt completion by the mean length of time required to complete that decile of molt. The mean duration of each decile of molt was estimated by comparing the mean date that birds were collected in initial (first 10 to 20%) and final (last 10 to 20%) stages of each decile of molt during each year of the study and averaging over all years (see Heitmeyer, 1987 for calculations of mean duration of the entire prebasic molt).

RESULTS

The mean dry mass of the basic plumage of adult female Mallards was 72.7 ± 0.3 (SE) g (Table 1). All body feathers except the primaries, secondaries, primary and secondary coverts, wing lining, and axillaries are replaced during the prebasic molt (Heitmeyer 1987). The dry mass of this newly replaced basic plumage was 53.65 ± 0.3 g (Table 1).

Approximately 46 g of protein were deposited in the basic plumage of an average female Mallard (53.65 g of feathers \times 86.2% protein), and 84 g of ingested protein were required to synthesize this plumage (at 55% overall efficiency of dietary protein use). The cumulative replacement (g) of feathers (denoted as FG) was best expressed as an exponential curve ($FG = 7.69e^{0.02X}$, $R^2 = 0.85$, where X = percentage molt completion). More (Kruskal-Wallis tests, $P < 0.01$) feather mass was replaced during 11 to 50% completion (Table 2), but molting was more ($P < 0.01$) rapid during 41 to 70% completion (Fig. 1) than during other stages of molt. When grams of feathers replaced/decile were extrapolated to grams of protein required/day/decile more ($P < 0.01$) protein was required from 41 to 70% molt completion than at earlier or later stages (Fig. 2).

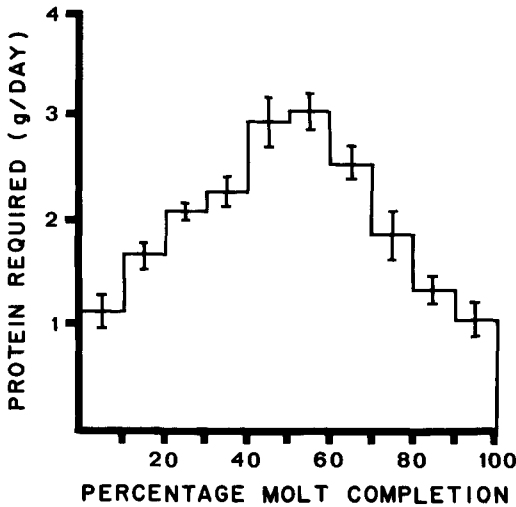


FIGURE 2. Mean grams of protein required/day to synthesize feathers during each decile of the prebasic molt of adult female Mallards collected in Missouri, 1981 to 1983 assuming a 55% overall efficiency of protein utilization. Vertical bars indicate standard errors.

DISCUSSION

Protein costs of the prebasic molt of female Mallards were higher during the middle stages of molt because chest-center, chest-side, and belly feathers, which compose a large portion of the total feather mass, molt more rapidly at this time (Heitmeyer 1987). The protein cost curve (Fig. 2) closely resembles the curves of net energy costs and nitrogen retention of molting White-crowned Sparrows (Murphy and King 1984a: 319-320, 1984b:327) and the rate-intensity curve of feather replacement in female Mallards (Heitmeyer 1987).

The daily and total protein cost of the prebasic molt of female Mallards were substantial. The daily cost was especially high during the mid-portions of the molt when costs approach 3 g protein/day. This represents a significant increase above maintenance requirements (ca. 3.9 g/day for a 1,050-g female Mallard [using the equation of Scott et al. 1976:81, see also Robbins 1981]) and in proportion to total body protein (total body protein = 160 to 174 g excluding feathers, Heitmeyer 1985).

For female Mallards, the protein cost of molt is probably exceeded (as an annual event cost) only by protein requirements for reproduction. An average Mallard clutch of 11 eggs contains 69 g (dry weight) of protein with costs incurred over ca. 18 days (Krapu 1981). Similar to female Mallards engaged in the prebasic molt, female Mallards obtain most protein for egg laying by increased consumption of invertebrates and not from labile protein reserves (Swanson et al. 1979, Krapu 1981); therefore, 125 g of exogenous protein are required to produce a clutch (assuming a 55% efficiency). In comparison, the prebasic molt deposits 46 g of

TABLE 2. Mean mass (g) of feathers replaced during each decile (% molt completion) of the prebasic molt of adult female Mallards collected in Missouri, 1981 to 1983.

Decile	n	$\bar{x} \pm SE$	Cumulative replacement
0-10	86	5.32 \pm 0.07	5.32
11-20	12	6.52 \pm 0.18	11.84
21-30	9	6.63 \pm 0.24	18.47
31-40	6	6.49 \pm 0.06	24.96
41-50	8	6.04 \pm 0.21	31.00
51-60	14	5.39 \pm 0.13	36.39
61-70	17	5.18 \pm 0.42	41.57
71-80	19	4.82 \pm 0.31	46.39
81-90	7	3.76 \pm 0.16	50.15
91-100	5	3.50 \pm 0.07	53.65

protein in feathers in 46 days and requires 84 g of exogenous protein for feather synthesis. Protein costs/day in reproduction exceed 5 g/day during early egg laying (eggs 1 to 7) but decline to <2 g/day from eggs 8 to 11 (see Ricklefs 1974, Drobney 1980 for calculation of protein cost/day). Therefore, the daily protein costs of feather synthesis during the prebasic molt may approach that of laying a clutch of eggs (at least compared to costs/day of laying the last 4 to 5 eggs).

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