

DOES THE WING MOLT CAUSE NUTRITIONAL STRESS IN LESSER SNOW GEESE?

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ABSTRACT.—To test the hypothesis that wing molt causes nutritional stress for geese and ducks, I investigated what effect wing molt has on nutrient reserves of adult Lesser Snow Geese (*Chen caerulescens caerulescens*). The study was done in 1971 and 1972 at the McConnell River (60°50'N, 94°25'W), Northwest Territories, Canada. Body weight, weight of body fat, dry weight of breast and leg muscle, and leg bone weight were used to index reserves. The data showed that these geese rely very little, if at all, on catabolism of body tissue to obtain nutrients for feather growth. Thus, I conclude that the molt does not cause nutritional stress for Lesser Snow Geese. I argue that this is predictable and suggest that it is true of other waterfowl. *Received 24 April 1978, accepted 3 October 1978.*

MOLT is a nutrient-costly process in birds (Payne 1972, King 1974). To meet that nutrient demand, a molting bird can use one or more of these tactics: 1) increase its daily nutrient intake, 2) make a compensatory reduction in other nutrient-demanding functions, or 3) catabolize body tissue.

The timing, duration, and pattern of molt vary greatly among bird species (King 1974: 9) and probably are important determinants of the tactic(s) used by a species. Birds that molt and regrow all flight feathers simultaneously apparently have a higher daily nutrient demand than those that have a sequential molt (King 1974: 37). Studies of energy intake by sequential-molters suggest that they use the first and/or the second of the above tactics (King 1974: 37–38). Canada Geese (*Branta canadensis*) are simultaneous-molters, and according to Hanson (1962) are unable to meet the demands of wing molt by increased food intake. Hanson argued that Canada Geese catabolize pectoral muscle and leg bone to get additional nutrients for wing-feather growth. Hence, he hypothesized (Hanson 1962: 13–14, Hanson and Jones 1976: 191) that molt, especially by females, is the most stressful period in the life cycle of waterfowl. Hanson (1962) did not define stress, but presumably meant *a situation in which a bird's nutrient demands exceed its nutrient ingestion, resulting in catabolism of body tissue*. That is how I define nutritional stress in this paper. But for such a situation to be stressful, in an evolutionary sense, the catabolism must result in a lowered fitness of the bird; Hanson (1962: 14) suggested that “the apparent differential stress of molt may be a primary reason for the preponderance of males in populations of adult waterfowl.”

Data are presented here to show that the dynamics of nutrient reserves in molting Lesser Snow Geese (*Chen caerulescens caerulescens*) are somewhat like those of Canada Geese. However, I argue that Hanson's hypothesis does not hold for Lesser Snow Geese and that these geese meet the nutrient demands of the wing molt through their food.

METHODS

Data are from geese collected in 1971 and 1972 at the mouth of the McConnell River (60°50'N, 94°25'W), Northwest Territories, Canada. MacInnes (1962) has described the area. As molt phenology and timing of collection periods were nearly identical in the 2 years (Table 1), the data were combined.

TABLE 1. Molt phenology and collection periods.

	1971	1972
Collected Late Incubation geese	26-27 June	19-26 June
Peak of Hatch	27-29 June	26-28 June
Collected Post Hatch geese	6-13 July	6-13 July
First flightless goose seen	16 July	15 July
Collected Early Molt geese	16-26 July	15-27 July
Collected Late Molt geese	28 July-7 August	1-8 August
First flying goose seen	10 August	12 August
Collected flying geese	10-18 August	15-17 August

Molting geese were collected in two ways: free ranging geese were shot by rifle, and every 20th goose was collected from flocks "rounded-up" during mass-banding drives (see Cooch 1956). Specimens were assigned to the following categories (Table 1): 1) *Early Molt*, geese collected during the first half of the wing molt period; 2) *Late Molt*, geese collected during the last half of the wing-molt period; and 3) *Flying*, post wing-molt geese (shafts of primaries and secondaries not blood-filled). All were collected with a rifle.

Dissection techniques were the same as reported in Ankney (1977a) and Ankney and MacInnes (1978). *Body weight*, i.e. the fresh weight of the goose minus intestinal contents, was used as an overall index of nutrient reserves. *Breast muscle* is the total dry weight of the *pectoralis*, *supracoracoideus*, and *coracobrachialis* muscles. *Leg muscle* is the dry weight of all muscles having either their origin or insertion on the femur or tibiotarsus. *Protein Reserve Index* (Protein R. I.) is the sum of leg and breast muscle. I present dry weights of muscles because water content, as a percent of total wet weight, is not constant but increases as muscle weight declines (Ankney, unpublished data). Thus, dry weight is a more accurate estimate of the muscle's protein content. *Body fat* is the total wet weight of subcutaneous, mesenteric, and abdominal fat (see Ankney 1974 for techniques). *Leg bone* is the fat-free dry weight of the femur and tibiotarsus. To remove fat, leg bones were broken and given two 24-h washings in 30 ml of chloroform in a shaker bath at 30°C. Change in leg bone weight is used as a crude index of changes in mineral composition. I have included for comparison data from *Late Incubation* geese (last 8 days of incubation) and *Post Hatch* geese (1-2 weeks after hatch) that have been reported elsewhere (Ankney 1977a, Ankney and MacInnes 1978).

I used *t*-tests to test for differences between two means; significance was set at the 5% level.

RESULTS

Lesser Snow Geese did not lose weight during the wing molt (Table 2). Mean body weight of females increased significantly between Late Incubation and Early Molt and that of males remained constant during the entire period.

TABLE 2. Mean (\pm S.E.) body weights, body fat weights, and leg bone weights (g) of adult Lesser Snow Geese collected before, during, and after the wing molt.^a

	Late Incubation	<i>P</i> ^b	Post Hatch	<i>P</i> ^b	Early Molt	<i>P</i> ^b	Late Molt	<i>P</i> ^b	Flying
<i>Body weight</i>									
Females	1,710 \pm 20	***	1,900 \pm 30	*	1,985 \pm 20	NS	2,010 \pm 20	NS	2,060 \pm 50
Males	2,250 \pm 40	NS	2,250 \pm 50	NS	2,250 \pm 40	NS	2,285 \pm 45	NS	2,285 \pm 40
<i>Body fat</i>									
Females	55.8 \pm 7.2		— ^c		— ^c		— ^c		— ^c
Males	46.1 \pm 6.1		— ^c		— ^c		— ^c		— ^c
<i>Leg bone</i>									
Females	23.7 \pm 0.5	***	19.3 \pm 0.5	***	22.6 \pm 0.6	NS	23.9 \pm 0.5	NS	23.7 \pm 0.9
Males	25.8 \pm 0.7	NS	24.3 \pm 0.7	*	26.8 \pm 0.8	NS	28.2 \pm 0.9	NS	29.4 \pm 1.0

^a Sample sizes are: Late Incubation = 41 females, 22 males; Post Hatch = 35 females, 22 males; Early Molt = 28 females, 18 males; Late Molt = 28 females, 14 males; Flying = 12 females, 6 males.

^b *P* = probability that means in adjacent columns are different by chance: * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001, NS indicates *P* > 0.05.

^c None of the geese in these categories had a measurable amount of Body Fat; see text.

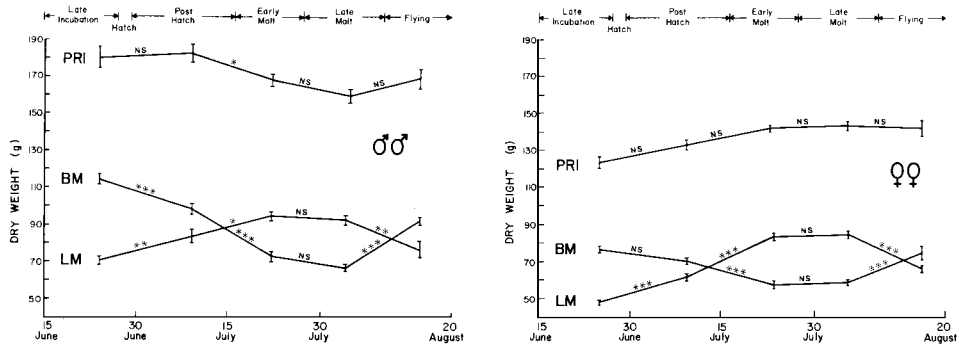


Fig. 1. Changes in dry weights of Leg Muscle (LM), Breast Muscle (BM), and Protein R. I. (PRI) of adult males (left) and females (right). Mean weights (± 1 S.E.) are plotted versus mean collecting date; see Table 1 for ranges of collecting dates. Sample sizes and symbols as in Table 2.

Mean body fat decreased from about 50 g in geese collected during Late Incubation to zero in geese collected during Post Hatch (Table 2). No Early Molt, Late Molt, or Flying geese had a measurable amount of body fat.

Mean leg bone weights of females declined between Late Incubation and Post Hatch but increased between Post Hatch and Early Molt (Table 2). Males showed a similar but less marked pattern. There was no change in mean leg bone weights of either sex during the wing molt.

There were large changes in mean breast and leg muscle weights, of both sexes, before, during, and after the wing molt (Fig. 1). These changes were always at least partially compensatory, i.e. a decrease in one muscle mass was accompanied by an increase in the other. The Protein R. I. of females did not change significantly between successive periods (Fig. 1). But the overall positive change between Late Incubation and Late Molt (124.3 g to 143.6 g) was highly significant ($P < 0.001$). The Protein R. I. of males decreased significantly between Post Hatch and Early Molt (Fig. 1).

DISCUSSION

To interpret these results and to evaluate the hypothesis about the great nutritional stress of molt, it is necessary to review the nutrient-reserve dynamics of nesting Lesser Snow Geese (reported elsewhere: Ankney 1977a, 1977b; Ankney and MacInnes 1978). Males and females arrive at the breeding grounds with large fat and protein reserves. Females rely on these reserves during egg-laying and incubation as they feed little then. Some females, near the end of incubation, starve to death; others desert their nests (to feed). Even females that successfully complete incubation are in poor condition: their mean body weight is 42% lower than that of females arriving at the breeding grounds, their fat reserves have declined by 89%, and their leg and breast muscle have declined by 22% and 40% respectively. Males also use fat and protein reserves during the egg-laying and incubation periods but rely mostly on fat (88% decline); their leg and breast muscles only decline by 8% and 16% respectively. The geese, particularly females, spend much time feeding after the eggs hatch (Harwood 1975). The male of a pair acts as a sentinel for the feeding female

and goslings; that is apparently a tactic that enables the female to recover from the stress of breeding.

Females began to recover after hatch as shown by increased body weight and Protein R. I. during Post Hatch and Early Molt (Table 2, Fig. 1). Male body weight did not increase then and Protein R. I. declined slightly. That decline resulted because leg muscle did not increase as much as breast muscle decreased (Fig. 1). But I do not think that the decline indicates nutritional stress in males. I suggest that because leg muscle of males had not declined as much as that of females did during nesting (see above) not as much increase was needed.

Why do these rapid, compensatory changes in leg and breast muscle occur? Hanson (1962: 20–23) noted similar changes in molting Canada Geese and proposed (p. 31) that hypertrophy of leg muscles resulted from extensive use but that atrophy of breast muscle was “an evolutionary adaptation . . . whereby these temporarily inactive muscles can be drawn on for vital constituents thereby maintaining a rapid rate of feather growth.” However, Hanson (Hanson and Jones 1976: 192) later realized that hypertrophy of the leg muscle begins before the onset of the flightless condition (as it does in Lesser Snow Geese; Fig. 1). He suggested that “the timing of the onset of the hypertrophy of the leg muscles and their subsequent development must . . . also be explained primarily on an evolutionary basis rather than on a purely functional use-disuse basis.” That is not the best explanation for the changes that occur in Lesser Snow Geese. Very soon after the eggs hatch (about 3 weeks before the onset of the wing molt) Lesser Snow Geese families walk to feeding areas, which are up to 50 km away at the McConnell River. There they spend about 20 h per day feeding (Harwood 1975) and often move several km during a day. But I have never seen undisturbed geese fly during that period—they are behaviorally flightless. Thus, not surprisingly, hypertrophy of leg muscle begins before the geese are flightless, and breast muscle, which began to atrophy after the geese arrived to the breeding grounds, continues to do so. The simplest explanation for that is the “use-disuse” hypothesis. Also, note the rapid changes in breast and leg muscle after the geese begin flying (Fig. 1).

There is no indication that Lesser Snow Geese *require* breast muscle protein for the formation of new feather keratin. It may be that some of the amino acids freed by the atrophy of breast muscle are incorporated into feathers; I think it more likely that they are used for the hypertrophy of the leg muscles (as suggested by Hanson and Jones 1976: 192). But the important point is that when the feathers are growing there is no evidence of a net protein deficit. This suggests that the birds are able to meet the protein requirement for feather growth directly from their diet.

That Lesser Snow Geese do not store fat during the wing molt is not evidence of stress but is predictable. They have a highly dependable food source (grasses and sedges, Harwood 1975) and their fall migration is 2 months away. To build and maintain unnecessary fat deposits would be energetically wasteful.

I cannot explain the decrease in mean leg bone weight of males and females that occurred during Post Hatch. Perhaps, as suggested by Hanson and Jones (1976: 192–193), the geese catabolize bone tissue to obtain phosphorus for the rapid hypertrophy of leg muscle. But there were significant increases in mean leg bone weight in both sexes between Post Hatch and Early Molt. This suggests that there was no mineral shortage when the geese were growing new wing feathers. However, as no histochemical analyses of the leg bones were done, I cannot say whether leg bone

weights accurately indicate changes in mineral composition. Hopefully, a future investigator will do such analyses and I predict that the results will show that geese (and ducks) do not require body minerals for feather growth.

Hanson's hypothesis about the great nutritional stress of molt for geese and ducks does not apply to Lesser Snow Geese. Hanson apparently based the hypothesis on data that were inadequate. He lacked data from breeding and pre-molt males, and from females during the last half of incubation and the interval between hatch and the wing molt (Hanson 1962: tables 13–16, 20, 21). Therefore any changes in nutrient reserves of the geese that might have occurred during those periods were undetected. Accordingly, the changes that occurred during the wing molt may have been incorrectly evaluated.

Lesser Snow Geese seem able to meet the nutrient demands of wing molt through their diet (tactic 1); the following argument shows why that is predictable even in the absence of data on adult geese. Consider that during the 6 weeks between the end of incubation and the end of wing molt, when adults replace their wing feathers, their goslings: 1) increase in body weight from 90 g to about 1,800 g (Cole and Ankney, unpublished data); 2) grow leg and breast muscles that are nearly adult size (Ankney, unpublished data); 3) grow and ossify a skeleton that is almost adult size (Ankney, unpublished data); and 4) *grow a complete set of body, tail, and wing feathers*. Adults and juveniles have similar diets (Harwood 1975). Thus, it is not surprising that adults can grow wing feathers without catabolizing body tissue. I suggest that other species of waterfowl behave similarly.

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