NUTRIENT RESERVE DYNAMICS OF BREEDING AND MOLTING BRANT

C. DAVISON ANKNEY

Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada

ABSTRACT.—I collected 150 Brant (*Branta bernicla*) at East Bay, Southampton Island, Northwest Territories, Canada, in 1979 and 1980 to evaluate how much these birds rely on reserves of fat, protein, and calcium during egg production, incubation, and the subsequent wing molt. Egg laying resulted in decreases in body weight and nutrient reserves of females. These decreases could have accounted for all of the fat but only 70% of the protein in an average clutch. Neither males nor females had sufficient reserves when incubation began to enable them to fast during that period. Only 11% and 22% of the energy required by males and females, respectively, could have been derived from their reserves during incubation. Brant evidently did not use body reserves to obtain nutrients for feather growth during wing molt. Rather, molting males and females accumulated muscle protein, which supports my hypothesis that wing molt is not a nutritional stress for waterfowl. *Received 12 August 1983, accepted 29 November 1983.*

IT is now generally thought that Arctic-nesting geese feed little during egg laying and incubation and that, consequently, stored nutrient reserves are the major determinants of clutch size and the ability of the female goose to complete incubation (Ryder 1970; MacInnes et al. 1974; Ankney 1977a, b; Ankney and MacInnes 1978; Raveling 1979a, b).

In order to test my hypothesis that the wing molt is not a nutritional stress in waterfowl (Ankney 1979), I collected male and female Brant (*Branta bernicla*) on Southampton Island, Northwest Territories, in 1979 during the egg-hatching period and throughout the subsequent wing molt. To my surprise, both sexes, but particularly females, seemed to be in much better condition at the end of incubation than are Lesser Snow Geese (*Chen c. caerulescens*). Also, in contrast to Snow Geese (Ankney 1977b), incubating Brant had been feeding before they were collected. Thus, in 1980 I returned to Southampton Island to collect Pre- and Postlaying Brant, to determine how much these birds rely on nutrient reserves for egg production and during incubation. This paper reports the results of that research and my evaluation of the importance of nutrient reserves to molting Brant.

METHODS

Adult Brant were collected by shooting or drive-trapping at East Bay (63°58′N, 81°50′W), Southampton Island. Birds were placed in the following categories for analysis (collection dates in parentheses):

Prelaying.—Females with several large ovarian follicles; males paired with such females (20 June).

Postlaying.—Females collected on the day, or day after, they laid their last egg, from nests with known histories; males paired with such females (26 June).

End of Incubation.—Birds collected from nests in which at least some of the eggs were pipped (12–13 July).

Post-hatch.—Birds collected on 22 July, 10 days after the peak of hatch.

Start of Molt.—Birds that had shed their primaries but had no emerged new feathers (28 July).

Early Molt.—Birds that had new-growing 9th primaries <40% ($\bar{x} = 35\%$) of the mean final size of the 9th primary ($\bar{x}$ final size for females = 21 cm, that for males = 22 cm) (5, 8 August).

Mid-Molt.—Birds that had new-growing 9th primaries 50–70% ($\bar{x} = 58\%$) of final size (13 August).

Late Molt.—Birds that had new-growing 9th primaries >75% ($\bar{x} = 81\%$) of final size; these birds could fly (19 August).

Only Late Molt birds showed evidence (slight) of body molt.

Birds collected in 1979 were weighed (nearest 10 g) and then treated as follows. Breast and leg muscles and the gizzard were removed, weighed, and placed in 10% formalin for later fat extractions (see Wyndham 1980). Following removal, abdominal fat (Woodhall 1978), liver, and pancreas were weighed to the nearest 0.1 g. The intestine was measured (nearest 1.0 cm) with a meter stick, and the contents were removed and weighed. The weight of the contents was subtracted from fresh body weight to give the weight reported here. The sternum was air-dried and weighed (nearest 0.1 g); both leg bones (femur and tibiotarsus) were saved for later fat extractions. In 1980, the above procedure was followed, and, also, the entire dissected carcass, minus feathers (and minus ovary and oviduct in females), was brought south in 10% formalin for fat extraction. All tissues were oven-dried at 95°C (Kerr et al. 1982) before fat extractions were done in a Soxhlet apparatus using petroleum ether. Fat extractions were done on leg bones, gizzard, breast muscles, and leg muscles for 1979 and 1980 birds and the remaining carcass for 1980 birds. The weight of fat extracted from the carcass was called "other body fat" (OBF) and was regressed on "abdominal fat + leg bone fat + leg muscle fat + breast muscle fat" ($AF + LBF + LMF + BMF$). The resulting equations were $Y = 7.87X^{0.80}$ ($r^2 = 0.85$, df = 15, $P < 0.001$) for males and $Y = 8.25X^{0.76}$ ($r^2 = 0.85$, df = 27, $P < 0.001$) for females, where Y is the weight of OBF and X is the combined weight of $AF + LBF + LMF + BMF$. These equations were used to calculate OBF for the 1979 birds. Total fat is the sum of X and Y and is reported here. Protein, herein, is the sum of the lipid-free dry weight of the gizzard, breast muscles, and leg muscles. The calcium index is the sum of sternum weight plus the weight of the fat-free leg bones.

Potential clutch size in Prelaying females was the number of large, highly vascularized ovarian follicles (Ankney and MacInnes 1978) and actual clutch size in Postlaying females was the number of postovulatory follicles.

The breeding seasons of 1979 and 1980 were not phenologically identical. The date of the first egg in 1979 was similar to that occurring in what Barry (1962) called an early season; the date of the first egg was about 5 days later in 1980. I am unable to assess whether or not that difference has introduced bias into my data, but I am confident that the patterns of nutrient use that I report are representative of breeding and molting Brant.

RESULTS

CHANGES DURING EGG LAYING AND INCUBATION

Females.—Brant arrived in peak numbers at East Bay during 10–13 June, 1980, when there was virtually 100% snow cover. Thus, fat and protein reserves of Prelaying females (20 June) must have been smaller than at arrival, because these reserves presumably were used for existence energy and for ovarian and oviducal growth. Potential clutch size of Prelaying females was 4.46 ± 0.14, and actual clutch size of Postlaying females was 3.88 ± 0.19; Postlaying females averaged 0.56 ± 0.04 large atretic follicles. Although females spent considerable time feeding during egg laying (K. Abraham pers. comm.), egg laying still resulted in a large decrease in body weight and nutrient reserves (Table 1). The average body weight loss (241 g) was accounted for by decreases in the variables that I measured (note that the water to protein ratio in muscle was approximately 3:1, so the 20-g loss of protein equaled about 80 g of body weight loss; see Table 2 for weight loss in reproductive tissue). Most (58%) of the protein loss was from breast muscles, which declined by 20%; leg muscle declined by 17% and gizzard by 25%.

Raveling (1979a) calculated that fresh eggs of Cackling Geese (*Branta canadensis minima*) contain 12.7% fat and 14.8% protein; I used those figures to estimate how much of the fat and protein in a Brant clutch was derived from body reserves during egg laying. The average weight of fresh Brant eggs in nests of the Postlaying females was 84 ± 5.6 g ($n = 62$), and, therefore, the average clutch (3.88 eggs) contained 41 g of fat and 48 g of protein. Ovaries of Prelaying females, however, contained about 78 g of yolk (Prelaying weight minus Postlaying weight, Table 2). If the yolk composition of Brant eggs is similar to that of domestic geese (36% fat, 18% protein, Romanoff and Romanoff 1949), then prelaying ovaries averaged 28 g of fat and 14 g of protein. Thus, if the conversion of somatic fat and protein to egg fat and protein were 100% efficient, then decreases in body reserves could account for all of the fat but not more than 60% of the protein deposited during laying. Even if all of the ovarian protein in Prelaying females had been derived from body reserves, only 71% (34 g/48 g) of the protein in a clutch would be derived from reserves. Liver declined in weight by 29% ($P < 0.001$) during egg laying and may have contributed some protein to egg formation (see Raveling 1979a). There were no changes ($P > 0.05$) in pancreas weight or intestine length.

Females used some body calcium during egg laying. Brant eggshells averaged 8.2 ± 0.1 g ($n = 61$); weight loss of leg bones and sternum would account for about one half of one egg shell.

Females began incubation with relatively small fat reserves (7% of body weight), and these declined by 67% during incubation. The birds had little visible fat at the end of incubation,

TABLE 1. Changes in body weight, in fat, protein, and calcium reserves, and in digestive organs of breeding and molting female Brant.

Variable[a]	Pre-laying ($n = 13$)	P[b]	Post-laying ($n = 16$)	P	End of incubation ($n = 12$)	P	Post-hatch ($n = 5$)	P	Start of molt ($n = 13$)	P	Early molt ($n = 8$)	P	Mid-molt ($n = 8$)	P	Late molt ($n = 9$)
Body weight	1,384[c] (33)	***	1,143 (24)	***	1,013 (21)	NS	1,105 (50)	NS	1,150 (21)	NS	1,112 (22)	NS	1,156 (16)	NS	1,202 (17)
Total fat	123.5 (11.0)	**	81.2 (5.1)	***	26.7 (3.9)	NS	15.6 (2.6)	NS	31.6 (5.0)	NS	20.2 (1.5)	*	26.9 (2.6)	NS	32.7 (3.5)
Total protein	99.0 (2.2)	***	79.0 (1.6)	NS	75.7 (2.1)	NS	83.2 (3.9)	NS	86.2 (1.5)	NS	87.7 (2.1)	**	96.5 (1.7)	NS	96.5 (1.6)
Breast	58.5 (1.3)	***	46.9 (1.1)	*	43.2 (1.3)	NS	40.3 (1.8)	***	31.4 (1.2)	NS	32.1 (1.4)	**	39.2 (1.1)	***	47.6 (0.7)
Leg	22.7 (0.6)	***	18.9 (0.4)	NS	19.2 (0.7)	**	25.8 (2.3)	***	37.9 (0.8)	NS	38.7 (1.1)	NS	38.1 (1.1)	**	32.1 (1.4)
Gizzard	17.6 (0.5)	***	13.2 (0.5)	NS	13.3 (0.5)	**	17.2 (0.9)	NS	16.9 (0.2)	NS	16.8 (0.8)	*	19.2 (0.6)	*	16.8 (0.6)
Calcium index	16.2 (0.6)	***	11.8 (0.5)	NS	11.9 (0.4)	NS	11.9 (0.5)	NS	11.7 (0.3)	NS	12.2 (0.4)	NS	12.1 (0.5)	NS	11.5 (0.4)
Liver	36.0 (1.7)	***	25.4 (0.8)	NS	24.0 (1.1)	***	33.1 (1.9)	NS	31.5 (0.8)	**	36.5 (1.5)	NS	37.3 (1.4)	NS	33.4 (1.9)
Pancreas	4.9 (0.3)	NS	4.5 (0.2)	NS	5.0 (0.2)	*	6.6 (0.7)	NS	6.9 (0.2)	NS	7.0 (0.3)	NS	7.5 (0.2)	NS	7.5 (0.2)
Intestine	212 (6)	NS	204 (5)	NS	196 (4)	NS	203 (6)	NS	201 (3)	NS	206 (4)	NS	203 (3)	**	219 (4)

[a] In g except intestine length, which is in cm.

[b] P = probability (from 1-way ANOVA) that means in adjacent columns are different by chance; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, NS indicates $P > 0.05$.

[c] Mean; values in parentheses are standard errors of mean.

Table 2. Ovary and oviduct weights (g) of Pre- and Postlaying female Brant.

	Prelaying (n = 13)	P^a	Postlaying (n = 16)
Ovary	84.8[b] (7.6)	***	6.5 (2.0)
Oviduct	49.3 (3.0)	***	22.2 (2.7)

[a] P = probability (from 1-way ANOVA) that means in adjacent columns differ by chance; $***P < 0.001$.

[b] Mean; values in parentheses are standard errors of mean.

and most remaining fat was probably structural. Body weight declined by 130 g (11%) during incubation, and this loss was accounted for primarily by declines in fat reserves (54.5 g), protein reserves (13.2 g), and the ovary and oviduct (28 g). None of the digestive organs decreased in size during incubation.

Males.—Body weight and composition of males changed little during the laying and incubation periods, except that fat reserves declined ($P < 0.001$) by about 60 g (65%) (Table 3). Protein reserves did not change during those periods. Intestine length remained constant, and, although the pancreas and liver declined ($P < 0.05$) in weight during egg laying, the pancreas increased ($P < 0.001$) in weight during incubation, and liver weight remained constant.

Changes During Post-hatch and the Wing Molt

Both sexes gained weight after hatch although the gain was more pronounced in males ($P < 0.01$) than in females ($P < 0.1$) (Tables 1, 3). Body weight fluctuations, mostly nonsignificant, occurred during the wing molt. By Late Molt, however, males were 22%, and females 19%, heavier than at hatch. Fat reserves fluctuated slightly, usually nonsignificantly, and by Late Molt, fat reserves of both sexes were little different from those at hatch. Neither sex showed changes in calcium reserves after hatch.

Digestive-organ size changed markedly after hatch, which reflected increased feeding by the geese then. In females, gizzard, liver, and pancreas weights increased but intestine length did not; these organs were relatively constant in size during molt and at Late Molt they were, except for the pancreas, simlar in size to those of Prelaying females. In males, pancreas and gizzard weights increased, as did intestine length, after hatch. Male digestive organs generally increased thereafter, and by Late Molt they were considerably larger than those of Prelaying males. The sizes of digestive organs of Late Molt males and females were very similar.

The most pronounced changes after hatch were in breast and leg muscle lean dry weight (Tables 1, 3). In both sexes, these changes, which began at hatch, were greatest during the wing molt and were mostly compensatory, i.e. when breast muscle declined, leg muscle increased and vice versa. For both sexes, however, there was a net increase in total protein during the wing molt, and the increase was greatest in females (Figs. 1, 2). I regressed total protein (Y in g) on primary length (X in mm) and obtained the following equations: $Y = 86.1 + 0.03X + 0.0002X^2$ ($r^2 = 0.36$, $P < 0.001$) for females ($n = 38$) and $Y = 107.0 - 0.184X + 0.0012X^2$ ($r^2 = 0.35$, $P < 0.001$) for males ($n = 33$).

Patterns of breast- and leg-muscle change, although similar, were not identical for males and females (Figs. 1, 2). In females, breast muscle was at its lowest weight, and leg muscle had ceased increasing by the Start of Molt. In males, leg muscle had also reached maximum weight by the Start of Molt, but breast muscle did not reach its lowest weight until Early Molt. In both sexes, leg muscle began to decline and breast muscle to increase after Mid-Molt. By Late Molt, however, breast muscles were still lighter and leg muscles still heavier than in Prelaying birds. This suggests that these muscles are not back to "normal" weight until, or after, the birds are fully capable of flight.

Discussion

Egg-laying and incubation.—Female Brant apparently depend less on protein reserves for egg production than do Lesser Snow Geese (Ankney and MacInnes 1978) and Common Eiders (*Somateria mollissima*) (Korschgen 1977). In those species, protein in an average clutch is equal to, *or less than*, the difference in body protein between Pre- and Postlaying females. That was not so for female Brant as, even under the assumption of 100% conversion efficiency, only 70% of the protein in an average clutch could have come from nutrient reserves. As in the above species and in Cackling Geese (Raveling

TABLE 3. Changes in body weight, in fat, protein, and calcium reserves, and in digestive organs of breeding and molting male Brant.

Variable[a]	Pre-laying (n= 8)	P[b]	Post-laying (n= 9)	P	End of incubation (n = 10)	P	Post-hatch (n = 6)	P	Start of molt (n = 7)	P	Early molt (n = 8)	P	Mid-molt (n = 8)	P	Late molt (n = 10)
Body weight	1,297[c] (25)	NS	1,269 (40)	NS	1,225 (26)	**	1,349 (30)	NS	1,292 (30)	NS	1,222 (22)	NS	1,269 (21)	***	1,400 (22)
Total fat	97.1 (7.5)	**	66.1 (5.8)	***	34.3 (1.9)	NS	35.4 (3.0)	*	49.5 (5.4)	*	35.5 (1.5)	NS	35.8 (1.4)	NS	41.5 (3.7)
Total protein	106.4 (1.1)	NS	102.8 (2.9)	NS	102.9 (2.1)	**	115.9 (3.4)	NS	106.8 (3.2)	*	98.2 (2.2)	*	106.0 (2.5)	NS	113.2 (2.4)
Breast	63.6 (0.6)	NS	61.1 (1.7)	NS	61.7 (1.3)	NS	58.5 (1.9)	***	43.8 (2.4)	**	35.6 (1.4)	**	43.3 (2.0)	***	56.0 (1.4)
Leg	27.9 (0.4)	NS	28.6 (0.9)	NS	29.3 (0.9)	***	39.7 (1.6)	*	46.0 (1.7)	NS	44.8 (0.9)	NS	41.8 (2.2)	NS	38.3 (1.0)
Gizzard	14.9 (0.9)	NS	13.1 (0.8)	NS	12.0 (0.4)	***	17.6 (1.0)	NS	17.0 (0.6)	NS	17.7 (0.4)	***	20.9 (0.6)	*	18.8 (0.5)
Calcium index	12.8 (0.3)	NS	12.6 (0.6)	NS	14.1 (0.5)	NS	14.1 (0.6)	NS	13.7 (0.6)	NS	13.6 (0.4)	NS	15.2 (0.7)	NS	14.4 (0.4)
Liver	30.9 (2.4)	*	25.0 (1.2)	NS	25.7 (1.2)	NS	28.6 (1.9)	NS	29.7 (1.3)	**	38.4 (1.8)	NS	37.3 (2.0)	NS	33.9 (1.1)
Pancreas	4.5 (0.3)	*	3.4 (0.3)	***	5.0 (0.3)	**	6.6 (0.3)	NS	7.1 (0.3)	NS	7.4 (0.3)	NS	7.9 (0.4)	NS	7.6 (0.4)
Intestine	189 (6)	NS	184 (7)	NS	185 (4)	*	200 (3)	NS	201 (3)	NS	200 (5)	NS	202 (3)	**	221 (5)

[a,b,c] As in Table 1.

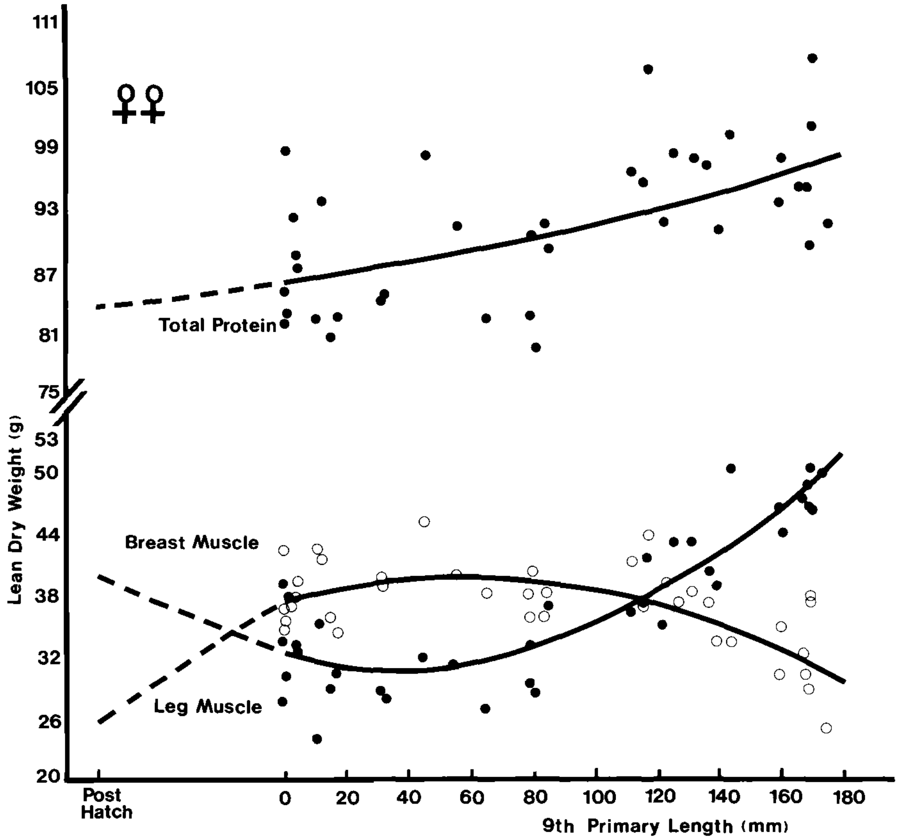

Fig. 1. Changes in lean dry weights of leg and breast muscle and in total protein of molting female Brant. Solid lines are from regressions of lean dry weight (Y) on 9th primary length (X): Breast muscle, $Y = 32.0 - 0.069X + 0.001X^2$ ($r^2 = 0.79$, $n = 38$, $P < 0.001$); Leg muscle, $Y = 37.3 + 0.081X - 0.0007X^2$ ($r^2 = 0.44$, $n = 38$, $P < 0.001$); total protein (see text). Dashed lines connect $\bar{x}$ values for Post-hatch birds with the Y-intercepts of the above equations.

1979a, b), however, all of the fat in an average Brant clutch could have been derived from nutrient reserves, assuming 100% conversion efficiency. During the Pre- to Postlaying interval male fat reserves also declined (30 g compared to 42 g in females). Assuming that this 30 g approximates maintenance costs during that period, the difference between the sexes (12 g) could have supplied the fat (13 g) deposited in the average clutch during that period. Female Brant are, thus, intermediate between Mallards (*Anas platyrhynchos*) (Krapu 1981), which use some body fat and little or no body protein for egg production, and the species mentioned above. Brant are also intermediate in body weight to those species, and I discuss the significance of that later.

Clearly, at the end of egg laying, neither male nor female Brant had sufficient reserves to enable them to fast during incubation. For example, the average female's 81 g of fat (= 729 Kcal) at the end of laying would last a fasting 1,062-g bird (1,143 − 81 g, Table 1) about 8 days based on Aschoff and Pohl's (1970) equation for BMR in nonpasserines. Females actually used only 70% of their body fat during incubation, whereas males used only 50%.

In Table 4, I show the patterns of reserve use during incubation for Brant, Cackling Geese, Lesser Snow Geese, and Common Eiders. [My calculations for Cackling Geese are slightly different from those of Raveling (1979b), as he used a different equation for males and a different value for the caloric content of protein;

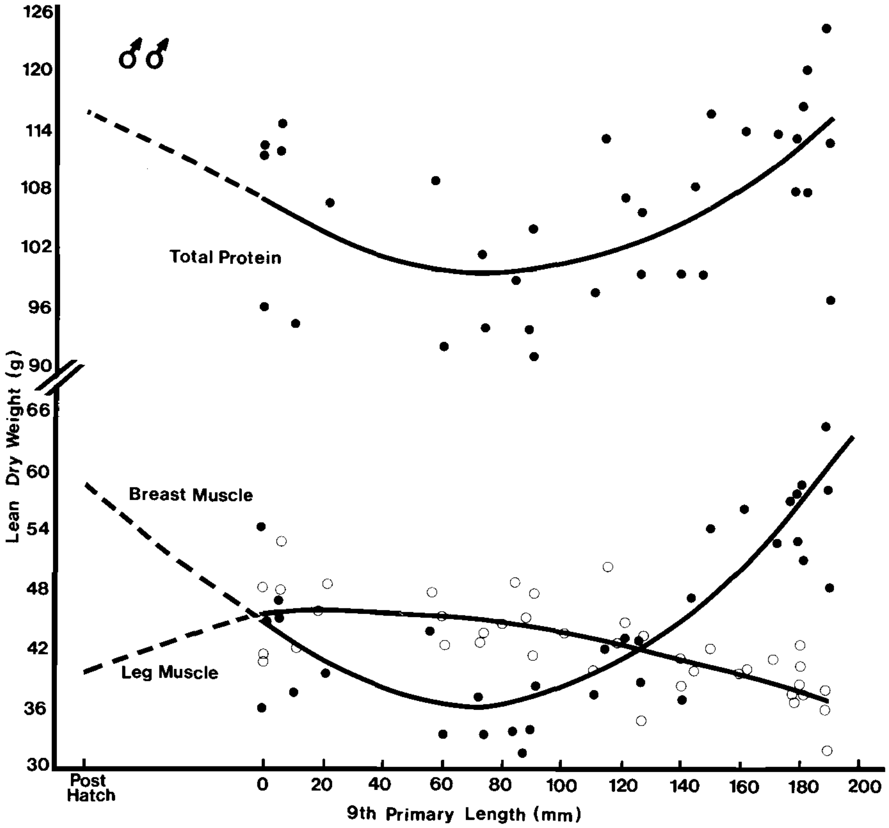

Fig. 2. Changes in lean dry weights of leg and breast muscle and in total protein of molting male Brant. Solid lines are from regressions of lean dry weight (Y) on 9th primary length (X): Breast muscle, $Y = 45.0 - 0.238X + 0.002X^2$ ($r^2 = 0.74$, $n = 33$, $P < 0.001$); Leg muscle, $Y = 45.8 + 0.012X - 0.0003X^2$ ($r^2 = 0.41$, $n = 33$, $P < 0.001$); total protein (see text). Dashed lines connect $\bar{x}$ values for Post-hatch birds with the Y-intercepts of the above equations.

his calculations for the requirements derived from reserves were 4% for males and 48% for females.] Only female Lesser Snow Geese and Common Eiders rely entirely on body reserves during incubation. Female Brant and female Cackling Geese clearly must feed considerably during incubation, and, consequently, the actual percentage of their energy requirements supplied by stored reserves (Table 4) is overestimated; the energy requirements shown in Table 4 are estimates for resting birds, and a more active bird (e.g. feeding) will have higher requirements. The reserves of female Brant and Cackling Geese may still be important, as the females, particularly of Cackling Geese, will be able to incubate more continuously than they could without them. Males of the three goose species do not fast during incubation, although male Lesser Snow Geese do derive a major portion of their energy requirements from stored reserves.

These patterns of reserve use during incubation by the three goose species are consistent with changes in digestive organs (Table 5; Korschgen did not present data for digestive organs of female Common Eiders but stated that the gizzard, liver, and intestine were small after laying and changed little during incubation). The largest declines in digestive organ size were in female Lesser Snow Geese; the largest increases were in male Cackling Geese. There were few or no changes in digestive organs of Brant.

The foregoing analysis shows that females of

TABLE 4. Energy requirements (Kcals) during incubation and energy derived from body reserves in some waterfowl.

Species[a]	$\bar{x}$ body weight (g)[b]	Requirements[c]	Energy[d] derived from: Lipid	Energy[d] derived from: Protein	Total	Total used/ total required	Weight loss (g)	Percentage loss
Brant								
Males	1,247	2,565	286	0	286	11%	44	3
Females	1,078	2,307	491	18	509	22%	130	11
Cackling Goose								
Males	1,495	3,172	28	149	177	6%	70	5
Females	1,241	2,769	1,242	126	1,368	49%	292	21
Lesser Snow Goose								
Males	2,465	3,513	2,035	198	2,233	64%	430	16
Females	2,120	3,131	2,830	253	3,083	99%	820	32
Common Eider								
Females	1,610	3,219	2,700	660	3,360	104%	620	32

[a] Sources of data: Brant, this study; Cackling Geese, Raveling (1979a); Lesser Snow Geese, Ankney (1977a), Ankney and MacInnes (1978); Common Eider, Korschgen (1977).

[b] Calculated as the mid-point of mean body weight at the end of egg laying and mean body weight at the end of incubation.

[c] Calculated from Aschoff and Pohl's (1970) equation for nonpasserines in the rest phase of the daily cycle.

[d] Based on 9.0 Kcal/g of lipid, 5.5 Kcal/g of protein (see Ricklefs 1974: 160).

only the larger waterfowl species have sufficient reserves at the end of laying to enable them to incubate without feeding, as previously suggested by Afton (1979: 46). There are at least two reasons why that is so. First, females of smaller species put *proportionately* more nutrients into eggs: in Brant the $\bar{x}$ clutch weight = 320 g = 23% of prelaying female body weight; in Cackling Geese the $\bar{x}$ clutch weight = 485 g = 26% of prelaying female body weight (calculated from data in Raveling 1979a); in Common Eiders the $\bar{x}$ clutch weight = 504 g = 20% of prelaying female body weight (calculated from data in Korschgen 1977); and in Lesser Snow Geese the $\bar{x}$ clutch weight = 488 g = 17% of prelaying female body weight (calculated from data in Ankney and MacInnes 1978). Fat reserves of postlaying females, as a percentage of body weight, averaged 7% for Brant, 12% for Cackling Geese, 18% for Common Eiders, and 15% for Lesser Snow Geese. Second, the metabolic/maintenance costs will

TABLE 5. Changes (%) in digestive organs of Brant, Cackling Geese, and Lesser Snow Geese during incubation.[a]

Species	Organ: Gizzard weight	Organ: Liver weight	Organ: Pancreas weight	Organ: Intestine length
Females				
Brant	+1%	−6%	+10%	−4%
Cackling Geese	+10%	−19%	—[b]	—[b]
Snow Geese	−27%	−43%	−27%	−18%
Males				
Brant	−8%	+3%	+47%	+1%
Cackling Geese	+30%	+30%	—[b]	—[b]
Snow Geese	−12%	+13%	+14%	+4%

[a] Sources of data: Brant, this study; Cackling Geese, Raveling (1979a); Lesser Snow Geese, Ankney (1977b).

[b] Not reported.

be proportionately higher for smaller females (see Calder 1974), i.e. even if postlaying Brant females had proportionately the same size lipid reserves as postlaying Lesser Snow Goose females, they would not be able to fast as long.

Clearly, there must be a minimum size below which a female is too small to be able to carry sufficient reserves for egg production and for all her maintenance energy during incubation. Lesser Snow Geese and Common Eiders are above that size, but note the very high use of protein by incubating eiders (Table 4); Brant and Cackling Geese are apparently below the minimum, as are Mallards [Krapu (1981: Table 1) showed that female Mallards are virtually devoid of fat reserves after 6 days of incubation]. Gatti's (1983: Table 2) summary of weight loss by incubating anatids (10 species) supports my argument, as it showed that the percentage of weight loss was proportional to body size, i.e. not only do females of larger species generally have absolutely larger reserves after egg laying, their reserves are also proportionately larger. My argument also is consistent with Afton's (1979, 1980) findings that incubation constancy in anatids generally increases with increased body size and supports his conclusion (1980: 136) that the relationship of fasting endurance to body size has been very important in the evolution of avian incubation strategies.

In tundra-nesting waterfowl, constant incubation is important in preventing nest loss to avian predators (Ryder 1970, Harvey 1971, MacInnes et al. 1974). How are Brant able to nest successfully when they cannot incubate continuously? I believe that they do so by nesting in a habitat that provides food immediately around their nest. The Brant at East Bay, as also reported by Barry (1962), nested immediately above the high-tide line in salt-marsh habitat dominated by goose grass (*Puccinellia spp.*) and sedges (*Carex* spp.). The Brant nesting area was the last area to become snow free in 1980, but, when it did, new growth of the vegetation had already begun. This habitat is markedly different from that used by the Lesser Snow Geese at East Bay, which nest farther inland on dry, lichen-covered ridges that became snow-free a week or more earlier than the area used by Brant (see Barry 1962). The habitat and areas in which the Brant nest are the same ones that they use for brood rearing. Thus, Brant, by nesting later than Lesser Snow Geese, are able to nest in areas that provide new green vegetation. Both sexes graze in the vicinity of the nest during egg laying and incubation (K. Abraham pers. comm.) and thus are able to return quickly to defend the nest if a predator appears. Snow Geese, however, would have to travel much farther from their nests if they were to feed.

Posthatch and wing molt.—Results reported here provide further support for my argument (Ankney 1979) that the wing molt is not a nutritional stress for waterfowl. There was no evidence, for either sex, that the birds catabolized bone to obtain feather constituents, e.g. chondroitin sulphate (Meister 1951) or phosphorus for the rapid hypertrophy of leg muscle (Hanson and Jones 1976: 192). That fat reserves remained small during the wing molt was predictable, as Brant have no need for large reserves then (see Ankney 1979: 71).

Males and females accumulated muscle protein simultaneously with growing new wing feathers. So, even though there were very great changes in breast and leg muscles before and during the wing molt, these changes did not result from the birds "raiding" their body tissues to obtain amino acids for feather growth. Young and Boag (1982) similarly found large compensatory changes in breast and leg muscles of molting male Mallards but no overall protein deficit. Raveling (1979a) reported that, during the early part of wing molt, male Cackling Geese showed no change in total protein content, females showed an increase, and both sexes showed compensatory changes in breast and leg muscle. These authors concluded that the birds' diet adequately provided the amino acids required for feather growth.

I previously argued (1979) that compensatory changes in breast and leg muscles of molting Lesser Snow Geese were best explained by a "use-disuse" hypothesis, i.e. these locomotory muscles hypertrophy when heavily used and atrophy when little used. Apparently, however, this does not adequately explain all such changes that occur in Brant. For example, in both males and females, breast muscles reached their lowest point just as the wing molt began and then increased by 57% in males and 48% in females by Late Molt. That cannot be due to increased use and thus appears to be an anticipatory change to ensure that the birds can fly when feather growth is complete. Ultimately, the change does relate to use-disuse but not as directly as I had supposed. Why breast muscle atrophies at all appears to be related to the rapid hypertrophy of the leg muscles that occurs after hatch: during the 15 days between hatch and the start of the wing molt, leg muscles increased by 17 g (57%) in males and 18 g (97%) in females, and breast muscles decreased by 18 g (29%) in males and 12 g (27%) in females. These changes must also ultimately be a "use-disuse" phenomenon, but they happen so fast that they may not be proximately due to "use-disuse." It seems more likely that the birds catabolize breast muscle to build leg muscle rapidly, as all of the increase in the leg-muscle weight of males and two-thirds of that of females can be accounted for by decreases in breast muscle.

ACKNOWLEDGMENTS

I thank D. Koval, W. Chappel, K. Bedford, K. Taylor, S. Johnson, D. Boyd, and, particularly, P. Kehoe and K. Maronets for lab and field assistance; H. Boyd and G. Cooch for advice and moral support; the Coral Harbour Hamlet council for permission to do research on Southampton Island; K. Abraham, D. Scott, D. Krementz, R. Alisauskas, A. Afton, and D. Raveling for helpful comments on the manuscript; and K. Abraham for talking me into going north "one more time." The research was supported by the Canadian Wildlife Service, U.S. Fish and Wildlife Service, Wildlife Management Institute, and the Natural Science and Engineering Research Council of Canada.

LITERATURE CITED

AFTON, A. D. 1979. Time budget of breeding Northern Shovelers. Wilson Bull. 91: 42-49.

———. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82: 132-137.

ANKNEY, C. D. 1977a. The use of nutrient reserves by breeding male Lesser Snow Geese *Chen caerulescens caerulescens*. Can. J. Zool. 55: 1984-1987.

———. 1977b. Feeding and digestive organ size in breeding Lesser Snow Geese. Auk 94: 275-282.

———. 1979. Does the wing molt cause nutritional stress in Lesser Snow Geese? Auk 96: 68-72.

———, & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95: 459-471.

ASCHOFF, J., & H. POHL. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29: 1541-1552.

BARRY, T. W. 1962. Effects of late seasons on Atlantic Brant reproduction. J. Wildl. Mgmt. 26: 19-26.

CALDER, W. A. 1974. Consequences of body size for avian energetics. Pp. 86-144 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club. No. 15.

GATTI, R. C. 1983. Incubation weight loss in the Mallard. Can. J. Zool. 61: 565-569.

HANSON, H. C., & R. L. JONES. 1976. The biogeochemistry of Blue, Snow, and Ross' geese. Carbondale, Illinois, Southern Illinois Univ. Press.

HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. Can. J. Zool. 49: 223-234.

KERR, D. C., C. D. ANKNEY, & J. S. MILLAR. 1982. The effect of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. Can. J. Zool. 60: 470-472.

KORSCHGEN, C. E. 1977. Breeding stress of female eiders in Maine. J. Wildl. Mgmt. 41: 360-373.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98: 29-38.

MACINNES, C. D., R. A. DAVIS, R. N. JONES, B. C. LIEFF, & A. J. PAKULAK. 1974. Reproductive efficiency of McConnell River small Canada Geese. J. Wildl. Mgmt. 38: 686-707.

MEISTER, W. 1951. Changes in histological structure of the long bones of birds during molt. Anat. Rec. 111: 1-21.

RAVELING, D. G. 1979a. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96: 234-252.

———. 1979b. The annual energy budget of the Cackling Goose. Pp. 81-93 *in* Management and biology of Pacific Flyway geese: a symposium (R. L. Jarvis and J. C. Bartonek, Eds.). Corvallis, Oregon, OSU Book Stores, Inc.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-297 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

ROMANOFF, A. L., & A. J. ROMANOFF. 1949. The avian egg. New York, John Wiley and Sons.

RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. Wilson Bull. 82: 5-13.

WOODHALL, P. J. 1978. Omental fat: a condition index for Red-billed Teal. J. Wildl. Mgmt. 42: 188-190.

WYNDHAM, E. 1980. Total body lipids of the Budgerigar, *Melopsittacus undulatus* (Psittaciformes: Platycercidae) in inland mid-eastern Australia. Australian J. Zool. 28: 239-247.

YOUNG, D. A., & D. A. BOAG. 1982. Changes in physical condition of male Mallards (*Anas platyrhynchos*) during moult. Can. J. Zool. 60: 3220-3226.