NUTRIENT RESERVES AND REPRODUCTIVE PERFORMANCE OF FEMALE LESSER SNOW GEESE

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ABSTRACT.—We studied the relation between nutrient reserves and reproductive performance of female Lesser Snow Geese (*Chen caerulescens caerulescens*) in 1971 and 1972 at the McConnell River (60°50′N, 94°25′W), Northwest Territories, Canada. We determined the potential clutch size of a pre-laying female by counting large (>20 mm), highly vascularized ovarian follicles; actual clutch size of post-laying females was the number of post-ovulatory follicles. Females with larger nutrient reserves had, on average, larger potential clutches. Reserves were used by the geese during laying and, after laying, the mean weights of reserves from females that laid different size clutches were not significantly different. We suggest that clutch size in Lesser Snow Geese is determined by size of nutrient reserves. Successful females used much of their remaining fat and protein reserves during incubation but this use was not significantly modified by the size of clutch they incubated. Late in incubation some females depleted their reserves and left their nests to feed; others starved to death. Thus, to reproduce successfully a female must retain, after egg-laying, sufficient nutrient reserves for her own maintenance during incubation. *Received 16 May 1977, accepted 14 October 1977.*

ARCTIC nesting geese feed little during egg-laying and incubation (Ryder 1970, Ankney 1977a). Ryder (1970) hypothesized that clutch size in these species evolved in relation to: (1) the energy reserves that the female accumulates before arriving on the breeding grounds, (2) egg size, and (3) the energy required to complete incubation. Harvey (1971) proposed that depletion of energy reserves was the major cause of nest desertion by female Lesser Snow Geese (*Chen caerulescens caerulescens*). As field data to test these ideas were lacking we investigated the importance of nutrient reserves to Lesser Snow Geese (both blue and white color phases).

Most previous studies of body reserves in breeding birds considered only fat (e.g. Breitenbach and Meyer 1959, Barry 1962, Harris 1970, Krapu 1974). However, we measured protein and calcium reserves in addition to fat (hereafter called nutrient reserves) because: (1) these are the major nutrients in an avian egg (Romanoff and Romanoff 1949), and (2) a fasting goose must metabolize body protein concurrently with fat (Benedict and Lee 1937, Hanson 1962). In this paper we discuss the relationship between the size of a female's reserves, her clutch size, and her ability to successfully complete incubation.

METHODS AND DEFINITIONS

Two summers (1971 and 1972) were spent at the nesting colony at the mouth of the McConnell River (60°50′N, 94°25′W), Northwest Territories, Canada. MacInnes (1962) has described the area. Females were collected from arrival on the breeding grounds to the start of the wing molt. The breeding phenology and timing of the collection periods were nearly identical in the 2 yr (Table 1). Birds were assigned to the following categories (Ankney 1974, 1977a, has described the collection methods and criteria for assigning birds to categories):

Arriving.—Females arriving on the breeding grounds.

Laying.—Females that had just completed laying. Some had an oviducal egg and no large follicles; the oviducal egg-weight was subtracted from the body weight.

TABLE 1. Breeding phenology and collection periods

	1971	1972
Peak of arrival	27 May–28 May	26 May–27 May
Collected Arriving ♀♀	23 May–29 May	23 May–31 May
Peak of Laying	28 May–3 June	27 May–2 June
Collected Laying ♀♀	30 May–1 June	30 May–7 June
Collected Early Incubation ♀♀	5 June–15 June	5 June–14 June
Collected Failed-nester ♀♀	—	22 June–24 June
Collected Late Incubation ♀♀	26 June–27 June	19 June–26 June
Peak of Hatch	27 June–29 June	26 June–28 June
Collected Dead ♀♀	27 June–2 July	29 June–1 July
Collected Post Hatch ♀♀	6 July–13 July	6 July–13 July

Early incubation.—Females that had incubated 6–11 days (all incubating geese were collected from nests with known histories).

Late incubation.—Females that had incubated at least 17 days of the 23-day incubation period.

Post hatch.—Females collected 7–14 days after the peak of the egg-hatching period.

Dead.—Females found dead or dying during the egg-hatching period.

Failed-nesters.—Females with incubation patches, collected away from the main part of the colony, near the end of the incubation period. We were unable to observe individual pairs of nesting geese and collect those that were inattentive to, or lost, their nests. Instead we collected birds that behaved as though they had lost their nest, or were away from their nest to feed. The decision to collect a particular goose was based on two criteria: (1) it was feeding with its mate and continued to feed for at least one-half h, and (2) it did not respond to gulls and jaegers in the manner shown by pairs that were near their nests. All such geese were included in the category Failed-nesters.

Body weight, the fresh weight of a goose minus the weight of intestinal contents, was used as an overall index of a female's nutrient reserves. The *Protein Reserve Index* (Protein R.I.) is the total dry weight of the sternal muscles (*pectoralis*, *supracoracoideus*, and *coracobrachialis*), leg muscles (all muscles having either their origin or insertion on the femur or tibiotarsus) and gizzard (minus contents). The *Fat Reserve Index* (Fat R.I.) is the total wet weight of subcutaneous, mesenteric, and abdominal fat. The *Calcium Reserve Index* (Calcium R.I.; calculated in 1972 only) is the total fat-free dry weight of the leg bones (femur and tibiotarsus) plus the sternum. Sternal and leg muscles were excised unilaterally and dry weights were doubled to compute protein reserves. Muscle tissues were freeze-dried in 1971 and oven-dried in 1972; these two techniques did not remove significantly different amounts of water from comparable samples (Ankney 1974). Intracellular fat in the muscles was considered a constant because Hanson (1962) showed that variation in intracellular fat content of leg and breast muscles of Canada Geese (*Branta canadensis*) accounted for very little of their gross weight changes (see also Hoar 1966: 226). In some females the sternum, or a leg bone, was badly shattered during collecting and calcium reserves could not be indexed; thus sample sizes are not uniform. Culmen lengths, measured as described by Godfrey (1966), were used to index structural size (Beer and Boyd 1962, MacInnes 1966, Ankney 1977b).

Potential clutch size of an Arriving female was determined by counting the large (>20 mm) ovarian follicles. There was an obvious size gap between the two to six large, highly vascularized follicles and the numerous non-vascularized small (<10 mm) follicles (Fig. 1; see also Wood 1964). Several Arriving females had an oviducal egg and one post-ovulatory follicle (Fig. 1); in these females potential clutch size was the number of large developing follicles plus one. In post-laying females *actual clutch size* was determined by counting the number of post-ovulatory follicles. These follicles were readily counted by eye in Laying and Early Incubation females; in Late Incubation, Failed-nesters, and Dead females they were counted through a binocular microscope at 15× magnification (after Kabat et al. 1948: 415). This method was determined to be accurate by comparing, in Late Incubation females, the number of counted post-ovulatory follicles from each female with the number of eggs in its nest when it had finished laying (Ankney 1974). Intact ovaries of Arriving and Laying females were weighed in 1972.

Statistical tests follow Sokal and Rohlf (1969).

RESULTS

Potential clutch size versus reserves.—The number of follicles that developed in a pre-laying female seemed to depend on her nutrient reserves (Table 2A). Heavier

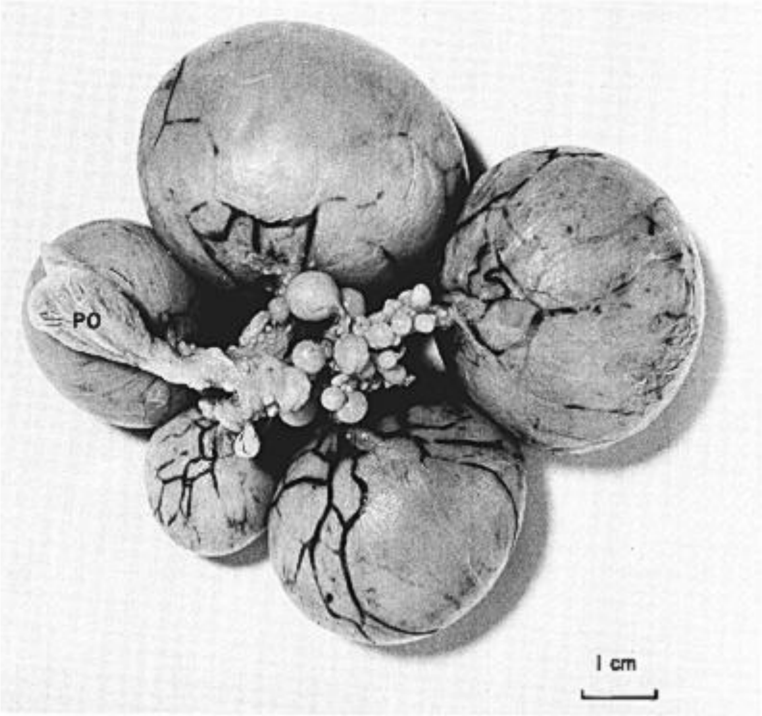

Fig. 1. Ovary (preserved in 10% formalin) of Arriving female. Note the vascularization of large follicles and the post-ovulatory follicle (PO) in this potential clutch of six eggs.

females, which had greater Fat, Protein and Calcium R.I.s, had larger potential clutch sizes (Table 2A). Little variation in body weight of Arriving females could be attributed to variation in ovary weight because: (1) the average weight of an ovary (N = 22, all potential clutch sizes represented) was only 102 g (3.5% of the average body weight), and (2) the weight difference between, for example, an ovary with five developing follicles and one with three developing follicles was approximately the weight of the two smallest follicles in the ovary with five (about 20 g).

Ryder (1970) postulated that female geese normally arrive on the breeding grounds with reserves as large as they can carry and still maintain long periods of flight. Thus structurally larger females should have larger reserves than structurally small females. There was a positive correlation between culmen length and body weight in Arriving females ($r = 0.553$; $P < 0.001$; df = 76). Thus about 31% of the observed body weight variation was explained by variation in structural size (r^2 equals the coefficient of determination, Sokal and Rohlf 1969: 503). Hence other factors were also important (see discussion). There was no correlation between culmen length and body weight in any other category of females except Post Hatch (when $r = 0.367$; $P < 0.05$; df = 33). It will be shown that after laying and during incubation all females were similar in weight because those which were heavier put more into egg production. Only after hatch, when females began to gain weight, would a correlation between structural size and body weight be expected.

The effect of egg laying on reserves.—The average body weight and the reserve indices were all significantly lower in Laying females than in Arriving ones (Table

TABLE 2. Body and nutrient-reserve index weights (g) of females with different clutch sizes

Clutch size[a]	Body weight		Protein R.I.		Fat R.I.		Calcium R.I.	
	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
A. Arriving females								
Two	3	2,400 ± 60	3	204.6 ± 8.2	3	348.7 ± 56.1	2	34.9 ± 0.7
Three	13	2,710 ± 40	13	209.4 ± 4.4	13	442.9 ± 26.2	6	36.5 ± 1.1
Four	31	2,920 ± 30	31	226.7 ± 3.2	31	487.2 ± 13.6	23	41.2 ± 1.1
Five	25	3,080 ± 20	25	234.1 ± 4.5	25	543.6 ± 14.4	13	41.0 ± 1.1
Six	6	3,300 ± 30	6	254.4 ± 10.7	6	598.5 ± 19.5	4	45.0 ± 0.9
F statistic[b]		41.400***		7.229***		9.341***		3.418*
B. Laying females								
Two	2	2,460 ± 215	2	190.1 ± 8.7	2	430.9 ± 24.3	0	—
Three	9	2,490 ± 50	9	201.4 ± 5.4	9	358.9 ± 39.7	6	32.7 ± 1.7
Four	19	2,570 ± 40	19	196.4 ± 8.1	19	371.6 ± 17.2	12	35.8 ± 2.1
Five	11	2,520 ± 50	11	182.9 ± 9.0	11	373.7 ± 29.9	7	33.5 ± 2.0
Six	3	2,460 ± 80	3	192.4 ± 2.7	3	351.4 ± 25.0	2	29.5 ± 2.2
F statistic[b]		0.896 NS		0.420 NS		0.313 NS		1.012 NS
C. Early Incubation females								
Two	1	1,850	1	151.0	1	88.0		—
Three	7	1,960 ± 90	7	171.4 ± 12.4	7	154.7 ± 21.2		—
Four	16	2,120 ± 40	16	185.3 ± 5.3	16	184.2 ± 15.0		—
Five	8	1,970 ± 90	8	173.5 ± 7.4	8	197.3 ± 35.6		—
Six	1	2,130	1	191.0	1	158.0		—
F statistic[b]		1.317 NS		0.824 NS		0.774 NS		—
D. Late Incubation females								
Two	0	—	0	—	0	—		—
Three	10	1,710 ± 50	10	140.9 ± 6.1	10	50.4 ± 12.4		—
Four	17	1,670 ± 30	17	145.8 ± 7.2	17	52.5 ± 12.9		—
Five	14	1,740 ± 30	14	154.0 ± 5.1	14	63.3 ± 11.5		—
Six	0	—	0	—	0	—		—
F statistic[b]		0.971 NS		0.926 NS		0.294 NS	—	

[a] Potential clutch size for Arriving females, actual clutch size for the others

[b] From 1-way ANOVA. * $P < 0.05$, *** $P < 0.001$, NS = no significant difference among means

3). However, there were no significant differences in mean body weights, or mean Fat, Protein, and Calcium R.I.s among Laying females with different clutch sizes (Table 2B). Females with larger reserves at arrival had put more of their reserves into egg production than females with smaller reserves. For example, body weight loss of 4-egg females averaged 12% during laying and the average Protein R.I. declined by 13%, the average Fat R.I. by 24%, and the average Calcium R.I. by 13%; these weight losses averaged 25%, 24%, 41%, and 34%, respectively, for 6-egg females.

Of the 420-g average body weight loss during egg laying, 121 g was accounted for by fat utilization. The Protein R.I. decreased by 34 g dry weight, which was equivalent to 121 g wet weight. Mean Calcium R.I. decreased by 6.6 g and mean ovary weight decreased by 94 g (102 g at arrival to 8 g after laying). The difference (80 g) between average weight actually lost and that accounted for by the above variables was partially due to: (1) the oviducts, which were not weighed, probably lost some weight; (2) breast, leg, and gizzard muscles were only an index to total body protein and females undoubtedly used protein from other muscles; and (3) weights of leg bones and sternae only indexed total bone calcium utilization and females likely used calcium from other bones.

Reserve use during incubation.—We measured the changes in nutrient reserves of successful females (incubating or with a brood when collected) and in unsuccessful

TABLE 3. Changes in body and nutrient-reserve index weights (g) of females during breeding

	Arriving (N = 78)		Laying (N = 44)		Early Incubation (N = 33)		Late Incubation (N = 41)		Post Hatch (N = 35)
	Mean ± S.E.	P[a]	Mean ± S.E.	P[a]	Mean ± S.E.	P[a]	Mean ± S.E.	P[a]	Mean ± S.E.
Body weight	2,950 ± 50	***	2,530 ± 30	***	2,040 ± 40	***	1,710 ± 20	***	1,900 ± 30
Protein R.I.	227.8 ± 2.6	***	193.6 ± 5.5	*	180.1 ± 3.8	***	147.6 ± 3.6	**	163.3 ± 4.0
Gizzard	34.7 ± 0.6	***	28.8 ± 0.7	***	23.7 ± 0.6	***	21.0 ± 0.4	***	29.5 ± 0.5
Breast muscle	129.9 ± 1.8	***	108.2 ± 2.5	**	99.1 ± 2.8	***	77.3 ± 2.2	NS	71.7 ± 2.1
Leg muscle	62.8 ± 0.9	***	56.7 ± 1.2	NS	57.2 ± 1.4	***	49.2 ± 1.4	**	62.1 ± 1.9
Fat R.I.	491.7 ± 10.4	***	370.3 ± 15.8	***	177.4 ± 12.3	***	55.8 ± 7.2	—	[b]
Calcium R.I.[c]	40.6 ± 0.7	***	34.0 ± 0.9		—		—		—

[a] 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 $P > 0.05$

[b] Only one had a measurable amount of fat; see text

[c] N = 48 for Arriving and 27 for Laying females

females (Failed-nesters or Dead). Females lost weight rapidly during incubation (Table 3). Body weights of Late Incubation females averaged 67.6% of average Laying weight and only 58% of that of Arriving females. Fat and Protein R.I.s decreased 85 and 24%, respectively, during incubation. The weight of all three muscle masses decreased, though most of the decrease in Protein R.I. (67%) was in breast muscle.

Females resumed feeding after hatch (Ankney 1977a) and their mean body weight increased by 11% in about 10 days (Table 3). Remaining fat reserves were used during the first week after hatch; only one of 35 Post Hatch females had a Fat R.I. greater than zero (28 g). The average Protein R.I. increased after hatch but the three muscle masses showed different patterns. Gizzard weight increased ($P < 0.05$) during Post Hatch in response to the great increase in feeding (Ankney 1977a). Mean breast muscle weight continued to decrease (but not significantly, $0.1 > P > 0.05$), but leg muscle weight increased (Hanson 1962, found that post-nesting Canada Geese also showed hypertrophy of leg muscles and atrophy of breast muscles).

We compared the body weights and Fat and Protein R.I.s of females incubating different clutch sizes and found no significant differences among either Early or Late Incubation females that were incubating different numbers of eggs (Table 2C and 2D).

Although Failed-nesters were difficult to collect, eight were obtained in 1972. All had incubation patches. Four had some new feather growth indicating that they had lost their nests. The other four may not have lost their nests but their behavior indicated that they would have eventually (Harvey 1971).

We found 29 Dead (includes dying) females in 1971 and 142 in 1972. Although we searched a larger area in 1972 we estimated that the mortality was also much greater. Thirty-five Dead females were saved for analysis; 36 others were weighed in the field. These females appeared to have died, or be dying, of starvation. All were extremely emaciated; their keels protruded noticeably and the breast and leg muscles were greatly reduced. Some dead females were on or near nests containing pipped eggs in which the goslings were dead; others were near nests (theirs?) in which the eggs had hatched but neither goslings nor gander were present. Several were on nests or on the tundra "brooding" dead goslings. Still others were found dead or dying on the tundra away from a nest (their abdominal feathers were tinged yellow, characteristic of all females that have very recently hatched their eggs, resulting from contact with the wet yellow down of newly hatched goslings). Dying females were found wandering about the colony after the peak of hatch when most geese had moved from the colony to feeding areas; none were accompanied by a gander. Most were unable to fly and few were able to run. Those that could fly were unable to gain altitude and were easily caught by a dog. Live birds were taken to camp; all died within 12 h.

Unsuccessful females had no measurable fat reserves and had significantly lighter body weights and Protein R.I.s than successful females collected during the same 7-day period (Table 4). Failed-nesters were in better condition than Dead females. The overlap of body weights of successful and unsuccessful females (Fig. 2) shows that many females barely made it through incubation.

Unsuccessful females must have used too much of their reserves in egg production. To increase the sample size of successful females we combined Early and Late Incubation females and compared their mean clutch size to those of unsuccessful females (Table 5). The average clutch sizes of Failed-nesters and Dead females were

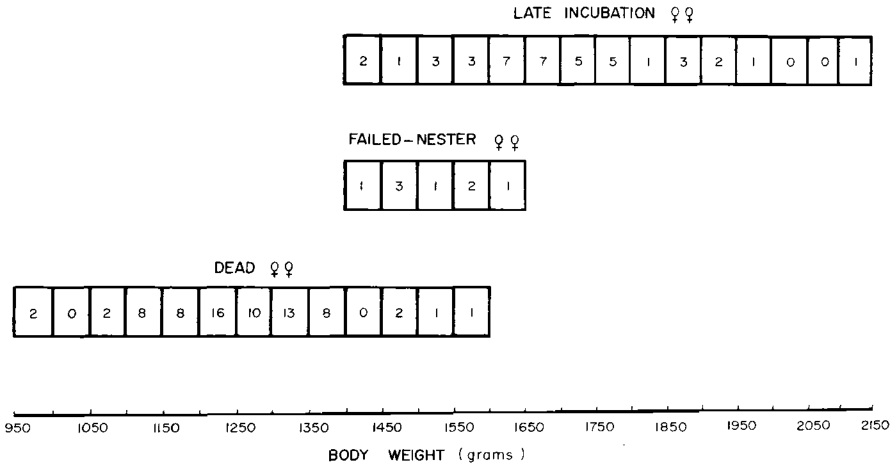

Fig. 2. Overlap in body weights of Late Incubation, Failed-nester, and Dead females. Numbers in boxes refer to number of females within that weight range.

smaller ($P < 0.01$) than that of successful females, but the means of Failed-nesters and Dead females were not different ($P > 0.05$, Table 5). The modal clutch size of successful females was four eggs (=45%), but that of unsuccessful females was three (=47%). Thus the nutrient cost of egg-laying averaged less in unsuccessful females. This suggests that they arrived on the breeding ground with smaller reserves than did successful females that laid the same number of eggs.

DISCUSSION

Nutrient reserves.—We have classified the body components we measured (depot fat, muscle protein, and skeletal calcium) as nutrient reserves. Many theories and studies concerning clutch size and incubation imply that food reserve means fat reserve (e.g. Lack 1968, Harvey 1971). Several authors (e.g. Connell et al. 1960, Odum et al. 1964) have stated that muscle protein is not utilized by birds and that the fat-free weight of a bird is relatively constant. Yet muscle protein has long been known to act as an amino acid reserve during periods of fasting or decreased food intake (Benedict and Lee 1937, Allison 1959, Hanson 1962, Anderson 1972). Fisher (1967) has shown that the domestic hen (*Gallus gallus*) can use stored protein for egg

TABLE 4. Comparison of body and nutrient-reserve index weights (g) of successful and unsuccessful females at late incubation time

	Successful (N = 41)		Failed-nesters (N = 8)		Dead (N = 35)[b]
	Mean ± S.E.	P[a]	Mean ± S.E.	P[a]	Mean ± S.E.
Body weight	1,710 ± 20	**	1,530 ± 30	***	1,250 ± 20
Protein R.I.	147.6 ± 3.6	**	120.4 ± 4.2	***	75.7 ± 1.9
Gizzard	21.0 ± 0.4	**	23.3 ± 0.8	***	18.9 ± 0.4
Breast muscle	77.3 ± 2.2	**	62.1 ± 2.3	***	32.5 ± 1.0
Leg muscle	49.2 ± 1.4	**	35.0 ± 1.7	***	24.2 ± 1.3
Fat R.I.	55.8 ± 7.2		[c]	—	[c]

[a] P = probability (from 1-way ANOVA) that means in adjacent columns different by chance. Symbols as in Table 3

[b] N = 71 for body weight

[c] None had a measurable amount of fat

TABLE 5. Clutch sizes of successful and unsuccessful females

	Failed-nesters (N = 8)	P^a	Successful[b] (N = 74)	P^a	Dead (N = 35)
Mean ± S.E.	3.13 ± 0.23	**	4.07 ± 0.09	**	3.44 ± 0.17
Range	2–4		2–6		2–6

[a] P = probability (from 1-way ANOVA) that means in adjacent columns different by chance; symbols as in Table 3. Mean clutch sizes of Dead and Failed-nesters not significantly different

[b] Early and Late Incubation

production whilst pectoral muscles serve as a protein reserve in the Red-billed Quelea (*Quelea quelea*) (Kendall et al. 1973, Jones and Ward 1976).

The importance of protein in egg production has been well documented (Scott 1973). Scott (1973: 53), referring to laboratory studies, stated that the female "can borrow to some extent from her body tissues when the diet is not adequate in protein or essential amino acids, although this ability to borrow is very limited and will allow her to produce only one or two eggs—and these eggs will be smaller than normal." Moss (1973: 59–66) pointed out the danger of applying laboratory studies, especially of domestic or semi-domestic birds, to field situations.

Females of many bird species lose weight during egg-laying. Harris (1970) suggested that weight loss in female Blue-wing Teal (*Anas discors*) reflected gonadal reduction and utilization of reserves, mostly fat. Hanson (1962) thought that weight loss in laying and incubating Canada Geese was a result of fat depletion. But Hanson's data (1962: 55) show that pectoral muscles of post-laying females averaged 14.5% lighter than those from migrating females (our calculations). Anderson (1972) found that hen pheasants (*Phasianus colchicus*) showed significant decreases in pectoral and leg muscle weights during egg-laying and proposed that this was a result of the high protein requirements of egg production. Certainly, reduced body weight in Laying female Lesser Snow Geese reflected fat utilization (29%) and gonadal regression (>24%), but a major portion resulted from the use of protein reserves (>29%).

Female Lesser Snow Geese seldom fly during egg-laying and not at all during incubation; walking is also restricted during egg-laying and especially during incubation. Thus, breast, leg, and gizzard muscles are little used (for the gizzard see Ankney 1977a) and can serve as protein reserves during incubation. Female Lesser Snow Geese are probably unusual in their heavy reliance on protein reserves during laying, and in their ability to maintain egg production despite very low intake of protein. But they undoubtedly share this ability with other artic-nesting geese that also feed little during egg-laying (see Ryder 1970, Ankney 1977a) and with certain penguins that fast during egg-laying (Richdale 1947). Perhaps in most species protein requirements during egg-laying are met by dietary proteins and the female does not utilize body protein (Krapu 1974, but see also Jones and Ward 1976).

Female Lesser Snow Geese, like some other birds, used skeletal calcium for egg production. Simkiss (1961) reported that medullary bone had been found in seven bird species including the Canada Goose and Mallard (*Anas platyrhynchos*); we observed medullary bone in the leg bones of female Lesser Snow Geese. The average weight loss in the bones we weighed (14.5%) was less than the maximum reported for chickens (40%; Taylor 1970). However, as chickens have undergone extreme artificial selection for egg production, they may have a greater ability to use skeletal calcium. That three of 44 Laying female Lesser Snow Geese had eggshells in their esophagi suggests calcium may be limiting in egg production. It seemed unlikely that these birds had eaten their own eggs or those of their neighbors (but see Ryder 1969). Rather, they probably ate shells from eggs predated by gulls or jaegers.

Nutrient reserves and clutch size.—Not only did female Lesser Snow Geese utilize nutrient reserves during egg-laying, but the extent of this use related to the number of eggs laid. Arriving females with more large developing follicles (larger potential clutch) were heavier and had significantly larger nutrient reserves than females with fewer large follicles. However, at the end of laying there were no differences between mean body weights or mean weights of Protein, Fat, and Calcium R.I.s from females that had laid different sized clutches. (The pattern in females with a clutch of two was not as above, but sample sizes were very small—three for Arriving and two for Laying.) These data strongly suggest that a female's clutch size was determined by the size of her nutrient reserves and imply that much variation in clutch size between females was caused by proximate rather than ultimate factors. They also support Ryder's (1970) hypothesis that arctic-nesting geese have evolved the ability to use the appropriate amount of reserves, for egg production, out of the total quantity available for all reproductive activities. Heretofore, only indirect evidence was available to support that idea: in several species of arctic-nesting geese, including Lesser Snow Geese, smaller than average clutches are laid in late seasons (Cooch 1958; Barry 1962, 1967); Barry (1962) showed that Atlantic Brant (*Branta bernicla*) were able to adjust their actual clutch downwards, during unfavorable seasons, by atresia of large follicles without subsequent development of new ones.

If, as Klomp (1970) argued, there is an "appropriate amount" of nutrient reserves to be committed to egg production, there must be other needs for the nutrients. Klomp suggested other reproductive activities and the most important must be incubation (Ryder 1970, Harvey 1971). Lesser Snow Geese never lay replacement clutches (Cooch 1958), yet they have not depleted their nutrient reserves after laying the first clutch. The implication is that they have utilized all that could be spared for egg production.

Nutrient reserves and incubation.—The amount of food reserves that the female requires to attend eggs during incubation presumably has been important in the evolution of clutch size in nidifugous birds (Ryder 1970, Klomp 1970). Harvey (1971) reported that female Lesser Snow Geese were accompanied by their mates if they left their nests, and were then apt to lose the nests to predators. This suggests strong selection for females that retain sufficient reserves to maintain maximum attentiveness to the eggs.

King's (1973: 101) statement that "it remains an open question as to whether or not a bird must significantly increase its energy expenditure for the specific purpose of incubating its eggs," cannot apply to female Lesser Snow Geese. Harvey (1971) experimentally determined that heat loss to the environment (including the eggs) was such that incubating Lesser Snow Geese always need to maintain metabolic rates above basal. Thus, we agree with Kendeigh (1973a: 113): "Heat loss to the eggs must be compensated for if the bird is to maintain its body temperature; to me this represents the energy cost of incubation." This energy cost probably explains why females utilized more reserves during incubation than did males (315 g versus 226 g of fat; 46.0 g versus 35.9 g of protein) even though females were probably less active than males (Ankney 1977c). Even in species in which the incubating female does not fast, considerable weight loss occurs (e.g., see Weller 1957, Oring 1969, Anderson 1972).

The total energy required for incubation is partially determined by clutch size (Kendeigh 1963). Why, then, were no differences detected in the nutrient reserve utilization by female Lesser Snow Geese incubating different size clutches? Eggs lose heat partly as a function of their weight (Kendeigh 1973b). There is great variation in egg weight within each clutch size in Lesser Snow Geese (Ankney and Bisset 1976). Variability in nest temperature was probably also important in obscuring differences: nests are built over permafrost that varies, within the goose colony, in depth below the surface. Also, some nests are thinly insulated and the eggs pressed into wet soil; others contain the eggs in thick layers of grass and down.

Late in incubation, females (Failed-nesters) were collected feeding away from their nests. They had utilized all their depot fat and their average body weight was 48% less than that of Arriving females. The Failed-nesters were in significantly poorer condition than females that were collected on or near their nests. This supports Harvey's (1971) hypothesis that late in incubation some females run out of reserves and become inattentive to, or desert the nest. Failed-nesters were, in effect, sacrificing their reproductive output for one season in favor of their own survival, a situation not unprecedented among birds (Drent 1973).

In both years of this study some females were found dead or dying during hatch; many were on or near nests and others had hatched a clutch. They showed no evidence of feeding (Ankney 1977a) and were in significantly poorer condition than either successful females or Failed-nesters. Their average weight was 58% less than that of Arriving females. That weight loss is greater than the 35–50% that Canada Geese, Mallards, and Ring-necked Pheasants can lose before starving to death (Jordan 1953, Hanson 1962, Anderson 1972). Had these females starved? They had pesticide levels too low to account for death (Ankney 1974). Disease or lead poisoning was rejected as the cause of death because: (1) no males were found dead, (2) deaths only occurred at hatch, and (3) external and internal examination revealed no pathological symptoms. Thus, we concluded that the females had died from starvation.

The higher mortality rate in 1972 may have resulted from the lower average air temperatures during incubation: 1.7°C in 1972 and 4.5°C in 1971 (Ankney 1974), although cloud cover and wind velocity (not recorded) are as important (Harvey 1971).

It is difficult to imagine why a female Lesser Snow Goose would remain on her nest until she starved. Harvey (1971) thought that incubation drive may be strong enough to cause that. Significantly, death only occurred right at or just before hatch—which in Mallards is the time of greatest acoustical communication between embryos and female (Hess 1972). Hess kept a female Mallard incubating a nest of infertile eggs for 4 weeks by playing recorded sounds of hatching ducklings. We heard peeping sounds from Lesser Snow Goose eggs that had not yet pipped. These sounds probably served, as in Mallards, to increase the female's attachment to her clutch.

As Lesser Snow Geese are iteroparous, selection is high against females that sacrifice themselves in favor of their brood, especially if the brood dies. Male Lesser Snow Geese are not known to incubate and when a female died before hatch the clutch was lost (many dead females were on or near nests that contained eggs with dead embryos or with partially hatched dead goslings). The fate of goslings from females that died after hatch was unknown. However, several lone ganders were observed with broods; their mates may have starved.

Ideally, a female Lesser Snow Goose should maintain maximum attentiveness to her nest but should leave it to feed rather than starve. Thus, Failed-nesters should be much more common than starved females. In 1972 we estimated that approximately 200 females had starved—a mortality rate of 0.1% (there were approximately 200,000 pairs of geese nesting at the McConnell River in 1972; Kerbes, pers. comm.). We have no data on number of females becoming Failed-nesters, but we calculate from Harvey's (1971) data that there were between 5 and 6% in 1967.

Causes of variation in nutrient reserves.—Variation in structural size (as indexed by culmen length) accounted for 31% of the body weight variation in Arriving females. This suggests that selection should favor increased body size in female Lesser Snow Geese. However, that would probably mean increased time to fledging, a consequence which might ultimately lower the fitness of larger birds. Arctic growing seasons are short and favor speedy development of young (Cooch 1958; Barry 1962; Ryder 1967, 1970).

Age may account for some variation in size of nutrient reserves between Arriving females. Prevett (1973) found that clutch sizes of 3- and 4-yr-old females were not different than those of older females. Most 2-yr-old Lesser Snow Geese do not nest (Cooch 1958); those that do nest lay smaller than average clutches (Prevett 1973). Maybe 2-yr-old females arrive on the breeding grounds with small reserves, possibly because estrogen production has not reached its peak. (Lemieux [1959] suggested that young female Greater Snow Geese (*Chen caerulescens atlantica*), nesting for the first time, were not in peak reproductive condition and produced small clutches.) Even if 2-yr-olds have reserves equivalent to those of adults it might be adaptive for them to committ less to egg production: nests of 2-yr-olds are not very successful (Prevett 1973).

Harvey (1971: 233) suggested that females with small reserves "may be individual variants physiologically unable to secure enough food during the months of feeding on the wintering grounds and on migration." Gunshot wounds during the previous hunting season might be a factor—routine dissection revealed that at least 31% of females carried lead shot (Ankney 1975a). Sublethal exposure to pesticides, lead poisoning, or other physiological or psychological stress could all have reduced a female's ability to store or maintain nutrient reserves. For example, a higher than expected proportion of the females we neckbanded in 1971 were found dead or dying in 1972 (Ankney 1975b, 1976). Neckbands may have contributed to the starvation of females because they caused the pre-arrival female to spend less than the optimum amount of time feeding (Ankney 1975b).

We think it unlikely that clutch size in Lesser Snow Geese is genetically controlled such that females put on only enough reserves to lay a predetermined number of eggs. If it were true, females would tend to lay the same size clutch every year; we have no data on this for Lesser Snow Geese but MacInnes et al. (1974) found considerable year-to-year variation in clutch sizes of individual Canada Geese at the McConnell River. Also, it would not make sense for females to arrive on the breeding grounds with less nutrient reserves than they could carry. Finally, except for Koskimies' (1957) suggestion that clutch size variations are the result of genetic polymorphism having adaptive value, it is generally thought that intrapopulation differences in clutch size of waterfowl are mainly the result of proximate influences (Johnsgard 1973).

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