

THE ANNUAL CYCLE OF BODY COMPOSITION OF CANADA GEESE WITH SPECIAL REFERENCE TO CONTROL OF REPRODUCTION

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ABSTRACT.—Fluctuations in weight, lipid, and protein content of the body, breast muscles, and liver and changes in the size of leg muscles, gizzard, and intestines of adult Cackling Geese (*Branta canadensis minima*) were determined for specimens collected during autumn migration, winter, spring migration, arrival at nesting areas, egg laying, incubation, and molting time periods. Both sexes lost most of their lipid stores in winter. Larger-sized races of Canada Geese maintain a store of fat during winter even though they lose as much or more weight as Cackling Geese. Differences in amounts of fat storage in relation to body size, climate severity, and the frequency with which food shortages may occur may limit the northern boundaries of the winter range in this and other species that conform to Bergmann's Rule.

At the time of their arrival on nesting grounds, body weights of males and females had increased 25.8% and 45.9%, respectively, over their weights in April. Females gained 1.8 times more weight, 2.4 times more fat, and 1.4 times more protein than did males. By the onset of incubation, 17 days after their arrival on nesting grounds, both sexes had lost weight nearly equivalent to amounts gained prior to their arrival. Lipid reserves of males were used by the onset of incubation, but were sufficient in females to maintain them until the end of their 26-day incubation period. Total protein in males was nearly maintained from the time of their arrival to the end of incubation, whereas it declined 22.7% in females between the time of arrival and the onset of incubation. At the time of hatching of their eggs, females had lost 42.1% of their peak spring weight, and they were emaciated.

The reserves stored by geese during spring migration allow them to initiate nesting before food supplies become abundant and are critical in controlling clutch size. The proximate mechanism causing cessation of egg laying appears to be depletion of some essential material(s) stored during the spring weight gain, probably protein. Gizzard, intestines, and liver are probably major sources of labile protein for egg production, and decline in weight of these organs lowers the metabolic cost of their maintenance while they are little used because of fasting during the period of reproduction.

Leg muscles of males hypertrophied throughout the spring and summer and were 92.6% heavier during the molt than during winter. Total protein of males during the molt, however, was not significantly different than during winter because of atrophy of breast muscles. Leg muscles of females hypertrophied only after hatching of their eggs. Breast muscles of females atrophied 18.6% during incubation and a further 14.3% during the molt, but total body weight, lipid, and protein levels of females were greater than at the end of incubation. Males nearly maintained their weight during the incubation period, while females were fasting. After hatching, females are obligated to feed nearly continuously because of their emaciated condition, while males can spend more time on the alert because of their better body condition maintained during the incubation period.

Received 13 March 1978, Accepted 12 December 1978.

LACK (1967) proposed that the clutch size of precocial waterfowl (Anseriformes) evolved in relation to availability of food for the female at the time of egg laying, modified by the size of the egg (Lack 1968a, b). Geese, however, generally arrive on their nesting grounds before food is abundant, or even available, and egg laying occurs soon after snow and ice melt (see Raveling 1978 for recent review). Peak body weights and fat reserves of geese occur just prior to their arrival on breeding areas (Hanson 1962a, Barry 1962, Ryder 1967, Ankney 1977a, Ankney and MacInnes 1978). Ryder (1970) modified Lack's proposal to conclude that clutch size of

arctic geese evolved in relation to accumulation of sufficient food to provide reserves for reproduction prior to arriving on nesting areas.

Raveling and Lumsden (1977) modeled the energetics of egg laying and incubation of Canada Geese (*Branta canadensis interior*). They refined Ryder's (1970) model and concluded that egg laying ceased when body weight declined to winter or "basal" levels, and that maximum reserves had been allotted to eggs. Proximal control of clutch size, therefore, lay in the depletion of some essential material(s) stored in the body.

Although there has been much recent emphasis on the energetics of reproduction (e.g. King 1973, 1974; Ricklefs 1974), there are few data on body composition in relation to various activities, especially immediately before and after egg laying. Jones and Ward (1976) suggested that protein reserve was the limiting factor in egg production by Red-billed Queleas (*Quelea quelea*), and Korschgen (1977) suggested that tissue protein from the digestive tract, especially the gizzard, may provide much of the protein requirements of the clutch of Common Eiders (*Somateria mollissima*). Ankney and MacInnes (1978) developed indices of lipid and protein reserves in Lesser Snow Geese (*Chen caerulescens caerulescens*) and concluded that the size of "nutrient reserves" controlled clutch size in that species. The purpose of this study was to determine changes in weight and lipid composition of the body and selected organs of Cackling Geese (*B. c. minima*) in relation to the requirements of varying activities. Geese were collected at precisely known stages of the annual cycle. Arctic geese make excellent subjects for such studies because they are relatively independent of environmental food supplies at the time of egg laying, lay only a single clutch, incubate nearly continuously, and are relatively well studied with respect to their natural history and daily activities, which are highly synchronized within a population.

METHODS AND MATERIALS

Adult geese (2+ years of age; Hanson 1962b) were collected by shooting or trapping during: 1) autumn and spring migration at Tulelake National Wildlife Refuge, Siskiyou and Modoc counties, California on 23 October 1973 and 4-5 April 1974; 2) winter at Sacramento National Wildlife Refuge, Glenn County, California on 27 December 1973; and 3) pre-nesting, nesting, and molting activities at Clarence Rhode National Wildlife Range near Old Chevak, Alaska on the Yukon-Kuskokwim Delta in May and June 1974, and July 1973 (see Mickelson 1975 for description of area). Summer specimens were collected between their time of major arrival (13 May) and the onset of egg laying (peak of nest initiation was 24-25 May); on the day of incubation initiation, which immediately follows the laying of the clutch; at the midpoint of incubation (day 13); and on the day that their eggs were hatching (day 26 of incubation).

Specimens were weighed on a Chatillon or Pesola spring scale and frozen until processed. Thawed specimens were reweighed. Retrices and remiges were pulled out by hand, the remaining feathers were removed with an electric sheep shears, and the weight of the shaved carcass was recorded. The digestive tract was removed and its contents were excised. Length and width of the left testis or ovary and largest ovarian follicles, and length of the small intestine, caeca (both combined), and large intestine were measured. Location and thickness of fat deposits were noted. The gizzard, liver, one-half of the breast muscles, and the muscle mass of one leg were weighed on an Ohaus triple beam balance.

The frozen (or partially so) carcass minus the liver and one-half of the breast muscles was cut into smaller pieces with a band saw. Carcasses were homogenized in a meat grinder. Liver and breast muscle samples were ground separately. Duplicate carcass samples of approximately 100-150 g and the entire ground breast muscle sample and liver were freeze-dried to constant weight (7 days). Values for breast muscle, liver, and carcass were proportioned to yield total body water and lipid content.

Body weight in this report refers to the ingesta-free, thawed weight (including feathers). Protein content of tissues was not measured directly, and the use of "protein" herein refers to the weight of dry, non-ether extractible residue, which of course includes the ash. Molt categories were defined by the length of the longest new-growing primary flight feathers (<35% = early molt and 43-48% = mid-molt).

Behavior of five pairs of geese during the egg-laying period could be observed from my tent. Behavior of two pairs of incubating geese was irregularly observed from a 4-m high tower.

Statistical comparisons were made with a one-way analysis of variance and comparison among means (Sokal and Rohlf 1969: 226).

RESULTS

ESTIMATION OF COMPOSITION OF PRE-LAYING GEESE AT PEAK WEIGHT

Composition of geese collected at their peak weight in mid-May during the pre-laying period could not be determined because of the breakdown of the freezer generator. Fortunately, these values can be reasonably estimated from the composition of spring peak weight gains measured in Giant Canada Geese (*B. c. maxima*), following Hanson (1965) (M. R. McLandress and Raveling, unpublished data). For adult males, 47.2% of the 1,425-g weight gain was fat, 35.5% was water, and 13.3% was protein (nonextractible residue). For adult females, fat made up 60.5% of the 1,321-g weight gain, water 20.7%, and protein 10.4%. The values do not add up to 100% because of increasing amounts of feathers. Applying these proportions to the weight gain of Cackling Geese and adding the values to the April levels of lipid, water, and protein content should closely approximate the real values. For comparison, the composition of male Giant Canadas changed during the month before egg laying from 14.2 to 22.8% lipid, 23.7 to 21% protein, and 55.5 to 50.4% water. Cackling Goose males in April averaged 13.8% lipid, 22.3% protein, and 56.8% water, and calculated peak weight values are 20.6% lipid, 20.4% protein, and 51.9% water (Table 1). Comparable figures for females are: Giant Canadas—17.6 to 29.1% lipid, 21.2 to 18.4% protein, 53.9 to 45.3% water; Cackling Geese—13.3 to 28.1% lipid, 20.4 to 18.6% protein and 57.0 to 45.6% water (Table 2).

BODY WEIGHT AND COMPOSITION (TABLES 1 AND 2)

Winter (October–April).—Both sexes lost weight between October and December, but the difference was significant only in males. Visible fat stores were nearly completely used (significant decline in both sexes), while protein (and hence water) levels were stable. Lipid levels were, however, 17 and 24 g greater in winter for males and females, respectively, than at hatching time. Lipid levels in midwinter were, thus, not much greater than what must be considered structural (e.g. phospholipids of cell membranes) and were certainly not the major source of energy for daily existence. Male geese, in fact, reached their minimum weight of the annual cycle in mid-winter. Significant increases in lipid content occurred in both sexes by April when spring migration had begun.

Arrival on nesting grounds.—The major arrival of Cackling Geese on the Yukon Delta occurred 12–13 May and was 12 days before the onset of egg laying and 17 days before the time that most of the breeding population began incubating (Raveling 1978). Pre-laying body weight of males had increased 33.8% from the winter low and 25.8% from early April, whereas females had gained 52.9% from midwinter and 45.9% from early April. Weight of pre-laying females exceeded that of males. Lipids increased from early April by 88.3% (181 g) in males and 209.3% (360 g) in females, while the protein increase was 15.4% (51 g) in males and 21.4% (62 g) in females.

Incubation onset.—The mean clutch size was 4.8 ($N = 66$) and the mode was 5. Cackling Geese lay an egg per day (Mickelson 1975). Four of the 5 females collected

TABLE 1. Body composition (g) of adult male Cackling Geese during the annual cycle.

Time	Body weight	Water content	Protein content	Lipid content
Autumn migration, 23 Oct., N = 9	1,540 ± 39 ^a (1,380-1,705) ^b	832 ± 12 (772-889)	328 ± 8 (281-350)	230 ± 20 (129-292)
<i>P</i> ^c	<0.01	N.S.	N.S.	<0.001
Midwinter, 27 Dec., N = 10	1,398 ± 33 (1,230-1,550)	835 ± 23 (706-939)	325 ± 7 (293-349)	70 ± 8 (33-123)
<i>P</i>	N.S.	N.S.	N.S.	<0.001
Spring migration, 5 Apr., N = 5	1,487 ± 53 (1,340-1,665)	844 ± 25 (762-911)	331 ± 11 (301-368)	205 ± 19 (157-265)
<i>P</i>	<0.001	N.T.	N.T.	N.T.
Pre-laying, N = 5	1,871 ± 38 (1,730-1,995)	971 ^d	382 ^d	386 ^d
<i>P</i>	<0.001	N.T.	N.T.	N.T.
First day of incubation	1,530 ± 37 (1,410-1,640)	974 ± 34 (911-1,030)	370 ± 13 (345-388)	56 ± 26 (26-107)
<i>P</i>	N = 5 N.T.	N = 3 N.T.	N = 3 N.T.	N = 3 N.T.
Mid-incubation, N = 1	1,455	937	356	46
<i>P</i> ^c	N.S.	N.S.	N.S.	N.S.
Hatch day, N = 6	1,460 ± 52 (1,315-1,665)	917 ± 28 (845-1,035)	343 ± 9 (306-373)	53 ± 9 (27-82)
<i>P</i>	N.S.	N.S.	N.S.	N.S.
Early molt, N = 9	1,443 ± 32 (1,260-1,605)	920 ± 21 (781-1,026)	324 ± 6 (295-358)	93 ± 11 (47-146)

^a Mean ± standard error of mean (g).

^b Values in () are ranges.

^c *P* = probability (from one-way ANOVA) that adjacent means within a row are significantly different. N.T. = no test because of insufficient sample sizes; N.S. = nonsignificant.

^d Calculated values—see text.

^e Compares first day of incubation with hatch day values.

at the onset of incubation had laid 5 eggs and the fifth had laid 6 eggs. After egg laying, the body weight of females had decreased 26.7% and they were 7.1% heavier than in early April. Weight of males had declined during these 17 days by 18.2%, and they were then only 2.9% heavier than in early April. The nature of the weight loss was different between the sexes, as 85.5% (330 g) of the lipids in males were used compared to 67.9% (361 g) in females, but females had accumulated a greater lipid reserve just prior to their arrival on the nesting grounds. Lipid levels of females at the onset of incubation were nearly identical to their early April condition, whereas males averaged even less fat than during midwinter. Body weight of males was greater than during midwinter, however, because the protein accumulation during spring was not appreciably used [3.1% (12 g) decrease from arrival]. In contrast, the protein level of females declined 22.7% (80 g) between the arrival and the initiation of incubation and was equal to the midwinter low.

End of incubation.—Weight of males did not decline significantly during incubation, but lipid levels were at their lowest point of the year. Females were emaciated at the time of hatching their eggs. They had lost 21.1% (292 g) of their weight during incubation and 42.1% (795 g) of their peak arrival weight (in 43 days). Lipids were essentially exhausted (138-g loss during incubation), and the 3.0% that remained must be considered essentially structural. Protein levels were at the lowest point of the annual cycle.

Molting.—Adult Cackling Geese lose their flight feathers about 2 weeks after their eggs hatch, and they are flightless for about 25 days (Mickelson 1975). Thus, geese in early molt were about 3 weeks past the time when hatching had occurred, and those in mid-molt were about 4 weeks past this period. Males lost a small but

TABLE 2. Body composition (g) of adult female Cackling Geese during the annual cycle.

Time	Body weight	Water content	Protein content	Lipid content
Autumn migration, 23 Oct., N = 6	1,287 ± 53 ^a (1,145–1,515) ^b	721 ± 22 (679–806)	276 ± 15 (227–320)	182 ± 24 (117–264)
<i>P</i> ^c	N.S.	N.S.	N.S.	<0.001
Midwinter, 27 Dec., N = 5	1,205 ± 33 (1,125–1,320)	719 ± 18 (671–780)	280 ± 9 (258–309)	57 ± 6 (34–71)
<i>P</i>	N.S.	N.S.	N.S.	<0.001
Spring migration, 5 Apr., N = 11	1,295 ± 47 (1,105–1,650)	738 ± 18 (656–848)	290 ± 7 (265–337)	172 ± 25 (68–362)
<i>P</i>	<0.001	N.T.	N.T.	N.T.
Pre-laying, N = 4	1,890 ± 9 (1,860–1,910)	861 ^d	352 ^d	532 ^d
<i>P</i>	<0.001	N.T.	N.T.	N.T.
First day of incubation	1,387 ± 61 (1,180–1,530)	781 (696–867)	272 (230–313)	171 (136–205)
<i>P</i>	N = 5 N.T.	N = 2 N.T.	N = 2 N.T.	N = 2 N.T.
Mid-incubation, N = 2	1,195 (1,165–1,225)	734 (716–751)	269 (259–278)	73 (72–74)
<i>P</i> ^c	<0.001	N.S.	N.S.	<0.001
Hatch day, N = 9	1,095 ± 37 (950–1,295)	702 ± 25 (599–825)	249 ± 7 (223–281)	33 ± 5 (14–51)
<i>P</i>	<0.001	<0.001	<0.001	<0.01
Early molt, N = 8	1,362 ± 54 (1,195–1,590)	861 ± 36 (749–1,023)	295 ± 8 (262–337)	108 ± 13 (62–179)
<i>P</i>	N.T.	N.T.	N.T.	N.T.
Mid-molt, N = 2	1,295 (1,290–1,300)	819 (791–847)	299 (295–304)	82 (48–115)

^{a,b,c,d,e} As in Table 1.

statistically nonsignificant amount of weight, but their lipid levels had increased 40 g (75.5%) since hatching day. Females, on the other hand, recovered quickly from their emaciated condition at the end of incubation [24.5% increase in weight even though they had lost feathers, 227.3% (75 g) increase in lipids, and 18.5% (46 g) increase in protein].

CHANGES IN MUSCLE MASSES

Fluctuations in weight of the breast muscles of males (Table 3) through the winter and spring gain to peak weight were generally similar to body weight changes, but the relative increase in protein (and thus water) was greater than the increase in fat as compared to the total body (Table 1). Accumulated lipids were used by the onset of incubation. Weight and protein content of male breast muscles remained above winter levels throughout the incubation period but dropped precipitously in the molt [decline of 35.5% (55 g) in weight and 36.9% (14.4 g) in protein]. The large decline in breast muscle weight (Table 3) was not evident in total body weight or protein (Table 1) because of the continual enlargement of leg muscles through the spring and summer (Table 4).

Total weight of breast muscles of females did not change significantly through the winter although there was a significant decline and then recovery of the small amount of lipids in these muscles (Table 5). Peak weight of breast muscles occurred just prior to egg laying. Accumulated lipids were not exhausted until the end of incubation, and weight of these muscles at the onset of incubation equaled their weight in April. An exception in comparison to the total body cycle was that breast

TABLE 3. Composition (g) of breast muscles (½) of adult male Cackling Geese during the annual cycle.

Time	Weight	Water content	Protein content	Lipid content
Autumn migration, 23 Oct., N = 6	146 ± 4 ^a (131-161) ^b	103 ± 2.6 (92.2-113.1)	36.6 ± 0.8 (32.9-40.0)	5.9 ± 0.5 (4.1-8.1)
<i>P</i> ^c	N.S.	N.S.	N.S.	<0.001
Midwinter, 27 Dec., N = 10	139 ± 5 (116-159)	99.4 ± 3.6 (82.4-116.1)	36.2 ± 1.0 (30.2-40.2)	3.0 ± 0.3 (2.2-5.3)
<i>P</i>	N.S.	N.S.	N.S.	<0.001
Spring migration, 5 Apr., N = 5	145 ± 4 (130-154)	102.0 ± 3.1 (91.3-110.0)	38.0 ± 0.9 (33.6-40.5)	4.8 ± 0.2 (4.3-5.4)
<i>P</i>	<0.001	N.T.	N.T.	N.T.
Pre-laying, N = 5	185 ± 5 (168-200)	130 ^d	47.0 ^d	7.9 ^d
<i>P</i>	<0.05	N.T.	N.T.	N.T.
First day of incubation	165 ± 5 (146-183)	118.7 ± 6.0 (107.6-132.7)	42.4 ± 2.5 (37.3-47.8)	3.0 ± 0.6 (2.0-4.4)
<i>P</i>	N = 5	N = 3	N = 3	N = 3
Mid-incubation, N = 1	148	107.6	37.6	2.5
<i>P</i> ^c	N.S.	N.S.	N.S.	N.S.
Hatch day, N = 6	155 ± 5 (151-173)	113.8 ± 3.8 (97.8-126.4)	39.0 ± 1.2 (33.0-41.8)	2.6 ± 0.4 (1.6-4.4)
<i>P</i>	<0.001	<0.001	<0.001	N.S.
Early molt, N = 9	100 ± 3 (88-114)	72.6 ± 1.9 (63.3-82.9)	24.6 ± 0.8 (21.6-28.3)	2.3 ± 0.2 (1.2-3.6)

^{a,b,c,d,e} As in Table 1.

TABLE 4. Weight (g) of the muscles of one leg of adult Cackling Geese during the annual cycle.

Time	Males	Females
Autumn migration, 23 Oct.	59 ± 1.5 ^a (51-65) ^b N = 9	49 ± 3.0 (41-60) N = 6
<i>P</i> ^c	N.S.	N.S.
Midwinter, 27 Dec.	54 ± 2.2 (41-61) N = 10	48 ± 2.7 (42-57) N = 5
<i>P</i>	N.S.	N.S.
Spring migration, 5 Apr.	63 ± 3.4 (54-75) N = 5	52 ± 1.8 (42-63) N = 11
<i>P</i>	<0.05	<0.05
Pre-laying	76 ± 2.9 (68-86) N = 5	60 ± 1.9 (55-65) N = 4
<i>P</i>	N.S.	N.S.
First day of incubation	85 ± 4.8 (71-97) N = 5	58 ± 3.2 (53-71) N = 5
<i>P</i>	N.T.	N.T.
Mid-incubation	89	57 (54-59) N = 2
<i>P</i> ^d	N.S.	N.S.
Hatch day	87 ± 4.3 (74-102) N = 6	55 ± 2.5 (48-70) N = 8
<i>P</i>	<0.001	<0.001
Early molt	104 ± 3.5 (92-116) N = 9	96 ± 2.6 (88-107) N = 7
<i>P</i>		N.T.
Mid-molt		93 (88-98) N = 2

^{a,b,c} As in Table 1.

^d Compares pre-laying with hatch day values.

TABLE 5. Composition (g) of breast muscles (½) of adult female Cackling Geese during the annual cycle.

Time	Weight	Water content	Protein content	Lipid content
Autumn migration, 23 Oct.	119 ± 5 ^a (102–137) ^b	83.6 ± 4.4 (72.5–97.1)	30.7 ± 2.2 (26.2–37.9)	4.3 ± 0.8 (2.3–6.8)
<i>P</i> ^c	N = 6 N.S.	N = 4 N.S.	N = 4 N.S.	N = 4 <0.05
Midwinter, 27 Dec., N = 5	123 ± 3 (117–133)	87.1 ± 2.1 (82.3–95.1)	33.1 ± 0.5 (32.2–35.3)	2.6 ± 0.2 (1.9–2.9)
<i>P</i>	N.S.	N.S.	N.S.	<0.01
Spring migration, 5 Apr., N = 11	129 ± 4 (107–150)	91.3 ± 2.8 (75.4–103.7)	33.7 ± 1.0 (28.6–40.0)	4.2 ± 0.3 (2.9–6.4)
<i>P</i>	<0.001	N.T.	N.T.	N.T.
Prelying, N = 4	155 ± 7 (131–170)	107.0 ^d	39.2 ^d	8.7 ^d
<i>P</i>	<0.01	N.T.	N.T.	N.T.
First day of incubation	129 ± 6 (106–144)	84.6 (76.8–92.4)	29.9 (25.4–34.5)	5.1 (3.9–6.3)
<i>P</i>	N = 5 N.T.	N = 2 N.T.	N = 2 N.T.	N = 2 N.T.
Mid-incubation, N = 2	120 (118–121)	86.8 (85.9–87.7)	30.2 (30.0–30.5)	2.7 (2.6–2.8)
<i>P</i> ^c	<0.005	N.S.	N.S.	<0.001
Hatch day, N = 9	105 ± 4 (94–125)	78.6 ± 3.0 (68.9–93.9)	25.3 ± 1.0 (21.1–29.5)	1.6 ± 0.2 (1.2–2.6)
<i>P</i>	<0.05	<0.01	<0.05	N.S.
Early molt, N = 8	90 ± 5 (75–114)	65.0 ± 3.9 (53.5–84.4)	21.5 ± 0.9 (19.4–28.1)	2.2 ± 0.3 (1.3–4.3)
<i>P</i>	N.T.	N.T.	N.T.	N.T.
Mid-molt, N = 2	91 (90–92)	67.0 (66.6–67.4)	22.6 (22.2–23.0)	1.6 (1.0–2.3)

^{a,b,c,d,e} As in Table 1.

muscles of females continued to decline significantly in weight (14.3%, 15 g) and protein (15%, 3.8 g) between the end of incubation and the time of molt (Table 5), while total body weight, lipid, and protein levels had increased (Table 2). As for males, a large part of the increase was due to a 74.5% increase in the size of the leg muscles (Table 4). Unlike males, however, that increase in females occurred after their eggs had hatched and not during incubation.

LIVER (TABLES 6 AND 7)

Weight of the liver of both males and females was significantly greater in April than in autumn or winter, primarily because of an increase in water and protein content (and/or glycogen stores). A further large increase in liver weight occurred before the geese reached the breeding grounds [17.1% (7 g) in males and 75.7% (28.6 g) in females]. This was mostly fat in males (4.9 g, but 326.7% increase, with only a 0.2 g or 1.8% increase in protein and/or glycogen), and both fat (6 g, 500%) and protein and/or glycogen (5.2 g, 55.3%) in females. While the weight of the liver of males exceeded that of females through the winter by 11 to 19%, liver weight of females just prior to egg laying was 36.6% greater than liver weight of males.

At the onset of incubation, weight of the liver of both sexes had declined to below winter levels and accumulated lipids had been used. During incubation, liver weight of males and females did not change significantly, although there was a significant further decline in the small lipid component in livers of females. Significant increases in weight, protein, and lipid content of females' livers occurred after hatching of their eggs but did not change significantly in males.

TABLE 6. Composition (g) of the liver of adult male Cackling Geese during the annual cycle.

Time	Weight	Water content	Protein content	Lipid content
Autumn migration, 23 Oct.	29.5 ± 1.3 ^a (26.3-38.3) ^b	21.3 ± 1.4 (18.1-27.8)	7.6 ± 0.4 (6.8-9.4)	1.1 ± 0.1 (0.9-1.5)
<i>P</i> ^c	N = 9 N.S.	N = 6 N.S.	N = 6 N.S.	N = 6 N.S.
Midwinter, 27 Dec., N = 10	31.6 ± 1.9 (22.8-39.1)	22.1 ± 1.3 (15.6-27.6)	8.6 ± 0.5 (6.4-10.9)	1.0 ± 0.1 (0.8-1.4)
<i>P</i>	<0.005	<0.01	<0.01	<0.001
Spring migration, 5 Apr., N = 5	40.8 ± 4.1 (33.6-55.8)	28.4 ± 2.4 (23.7-38.5)	10.9 ± 1.0 (8.4-15.0)	1.5 ± 0.2 (1.0-2.3)
<i>P</i>	= 0.05	N.T.	N.T.	N.T.
Pre-laying, N = 5	47.8 ± 3.1 (41-58)	30.4 ^d	11.1 ^d	6.4 ^d
<i>P</i>	<0.001	N.T.	N.T.	N.T.
First day of incubation	21.4 ± 2.1 (18.0-29.4)	16.4 ± 1.8 (13.6-20.9)	5.8 ± 0.8 (4.7-7.7)	0.7 ± 0.1 (0.6-0.8)
<i>P</i>	N = 5 N.T.	N = 3 N.T.	N = 3 N.T.	N = 3 N.T.
Mid-incubation, N = 1	37.4	26.9	9.4	1.2
<i>P</i> ^c	N.S.	N.S.	N.S.	N.S.
Hatch day, N = 6	27.8 ± 1.5 (20.9-31.4)	19.8 ± 1.0 (14.7-22.9)	7.2 ± 0.3 (5.6-7.8)	0.9 ± 0.04 (0.7-1.0)
<i>P</i>	N.S.	N.S.	N.S.	N.S.
Early molt, N = 9	31.1 ± 1.5 (25.5-37.9)	22.0 ± 1.1 (18.1-26.7)	8.0 ± 0.4 (6.4-9.9)	1.0 ± 0.05 (0.9-1.3)

^{a,b,c,d,e} As in Table 1.

GIZZARD (TABLE 8)

Weight of the gizzard (empty) of males did not increase along with body weight to the pre-laying period (Table 1) as it did for females (17.7%, 11.6 g), but it declined significantly between the time of arrival on the breeding grounds and the onset of incubation in both sexes [19.2% (14 g) in males and 30.5% (23.5 g) in females]. Thereafter, gizzard weight of males increased significantly during incubation but not after hatching, whereas in females the increase during incubation was non-significant after hatching.

DISCUSSION

ESTIMATION OF PROTEIN CONTENT

I believe that the non-ether extractible residue of the samples provides a reasonable estimation of fluctuations in protein content, at least for relating patterns to the nature of varying activities of the annual cycle. This confidence is based on the parallel changes in residue and water in which the pattern for the entire carcass was also evident in muscle and liver tissues, which are primarily protein. For example, neither carcass (Table 1) nor breast muscle (Table 3) protein in males declined to winter levels by the onset of incubation, but it did in females (Tables 2,5). Milne (1976) found that ash weight of Common Eider carcasses did not vary significantly during the year in either sex.

The largest potential for error in protein estimation would seem to be in not

TABLE 7. Composition (g) of the liver of adult female Cackling Geese during the annual cycle.

Time	Weight	Water content	Protein content	Lipid content
Autumn migration, 23 Oct.	26.7 ± 1.3 ^a (21.9–30.4) ^b N = 6	16.9 ± 0.7 (15.2–18.3) N = 3	6.4 ± 0.3 (5.9–7.2) N = 3	0.7 ± 0.03 (0.7–0.8) N = 3
<i>P</i> ^c	N.S.	N.S.	N.S.	N.S.
Midwinter, 27 Dec., N = 5	27.7 ± 2.2 (23.0–34.6) <0.05	19.1 ± 1.3 (16.0–23.9) <0.005	7.8 ± 0.6 (6.3–9.7) N.S.	0.8 ± 0.09 (0.6–1.1) <0.001
<i>P</i>				
Spring migration, 5 Apr., N = 11	36.7 ± 2.1 (26.4–42.9) <0.001	26.1 ± 1.4 (18.2–33.7) N.T.	9.4 ± 0.5 (7.0–12.4) N.T.	1.2 ± 0.07 (0.9–1.8) N.T.
<i>P</i>				
Pre-laying, N = 3	65.3 ± 10.2 (50.0–90.0) <0.001	43.5 ^d N.T.	14.6 ^d N.T.	7.2 ^d N.T.
<i>P</i>				
First day of incubation	26.5 ± 2.8 (21.0–35.4) N = 5	21.0 (17.1–24.9) N = 2	7.1 (5.1–9.1) N = 2	1.2 (0.9–1.4) N = 2
<i>P</i>	N.T.	N.T.	N.T.	N.T.
Mid-incubation, N = 2	23.6 (21.5–25.7) N.S.	16.9 (15.3–18.4) N.S.	5.9 (5.4–6.4) N.S.	0.8 (0.7–0.8) <0.001
<i>P</i> ^c				
Hatch day, N = 9	21.4 ± 1.5 (18.0–32.6) <0.05	15.3 ± 1.3 (12.6–23.6) <0.005	5.4 ± 0.3 (4.8–8.1) <0.001	0.7 ± 0.02 (0.6–0.8) <0.001
<i>P</i>				
Early molt	30.2 ± 2.3 (21.0–39.0) N = 8	22.1 ± 1.8 (13.8–28.0) N = 7	8.3 ± 0.4 (6.1–9.9) N = 7	1.1 ± 0.04 (0.9–1.2) N = 7
<i>P</i>	N.T.	N.T.	N.T.	N.T.
Mid-molt, N = 2	29.6 (29.3–29.8)	20.7 (20.6–20.7)	7.8 (7.6–7.9)	1.1 (1.0–1.2)

^{a,b,c,d,e} As in Table 1.

accounting for skeletal changes in adult females, which form and lose medullary bone in the process of egg laying. However, medullary bone was apparently formed within a few days before egg laying and exhausted when the clutch was complete (Raveling et al. 1978). The average weight of the shell of a Cackling Goose egg is 8.77 g (N = 28, T. Roudybush, personal communication). Thus, an average clutch represents about 44 g of shell material or 55% of the 80-g loss of nonextractable remains that occurred between arrival and the onset of incubation in females (Table 2).

EFFECT OF CIRCADIAN RHYTHMS

Weight of the body and its constituents, especially the liver (Fisher and Bartlett 1957), fluctuates daily depending upon the activity rhythm of a species. These effects should not mask major patterns reported here, however, as they are relatively small in such a large bird as a Canada Goose. Additionally, most (83%, N = 46) of the geese in the October, December, and April samples were collected during their first feeding period within 2 h of sunrise. On the Alaska summer grounds, geese may be active at nearly anytime under the nearly continuous light, and samples were collected in midday (between 1000 and 1900) hours.

TABLE 8. Weight (g) of the empty gizzard of adult Cackling Geese during the annual cycle.

Time	Males	Females
Autumn migration, 23 Oct.	76.2 ± 3.1 ^a (62.0–89.9) ^b N = 9 N.S.	65.9 ± 3.3 (59.6–74.7) N = 2 N.S.
<i>P</i> ^c		
Midwinter, 27 Dec.	70.3 ± 1.9 (60.8–78.1) N = 9 N.S.	65.2 ± 4.2 (55.3–78.9) N = 5 N.S.
<i>P</i>		
Spring migration, 5 Apr.	74.1 ± 3.4 (67.3–86.8) N = 5 N.S.	65.4 ± 2.4 (55.7–83.7) N = 11 <0.05
<i>P</i>		
Pre-laying	73.0 ± 4.0 (66.0–83.0) N = 5 <0.01	77.0 ± 1.8 (72.0–81.0) N = 4 <0.001
<i>P</i>		
First day of incubation	59.0 ± 2.6 (53.8–67.8) N = 5 N.T.	53.5 ± 3.3 (45.0–64.7) N = 5 N.T.
<i>P</i>		
Mid-incubation	82.7 N = 1 <0.001	64.2 (55.1–73.3) N = 2 N.S.
<i>P</i> ^d		
Hatch day	76.6 ± 4.3 (64.0–88.8) N = 6 N.S.	58.7 ± 3.5 (48.6–72.2) N = 8 <0.001
<i>P</i>		
Early molt	81.6 ± 2.7 (67.5–93.5) N = 9	85.0 ± 3.8 (69.9–102.2) N = 8 N.T.
<i>P</i>		
Mid-molt		78.1 (76.7–79.5) N = 2

^{a,b,c,d} As in Table 1.

ECOLOGICAL ADAPTATIONS

Cackling Geese arrive in the Klamath Basin (Tulelake) in large numbers in mid-late October. By late November they have moved into the Central Valley of California where they remain through February. They migrate back into the Klamath Basin in March and depart from there by mid-April. The remainder of their migration is poorly understood, but they usually pass the Copper River Delta near Cordova, Alaska in large numbers between 28 April and 2 May (P. Islieb, personal communication). Major arrivals on the nesting grounds of the Yukon Delta occur in mid-May, egg laying proceeds during the last week of May and first week of June, hatching occurs in the first half of July, the flightless period of the molt lasts from mid- to late July through mid-August, and then geese gradually leave the Delta by early September (Mickelson 1975, Raveling 1978). Their autumn concentrations and migration routes between the Yukon Delta and their arrival in the Klamath Basin in late October are relatively poorly understood, except for a minor concentration that stops at the mouth of the Columbia River between Washington and Oregon (Nelson and Hansen 1959).

TABLE 9. Comparison of wing length (flat) to body weight of adult males of three subspecies of Canada Geese.

Subspecies	Weight (g)	Wing length (mm)	Proportions compared to <i>B. c. minima</i>	
			Weight	Wing length
<i>B. c. minima</i> ^a	1,540	385		
<i>B. c. interior</i> ^b	4,079	507	+165%	+32%
<i>B. c. maxima</i> ^b	4,880	511	+217%	+32%

^a Weight from Table 1; wing length from unpublished data, N = 19.

^b From Hanson (1965: 20, 27).

Winter (October–April).—The decline in body weight of 9.2% in males and 6.4% in females from October to December was not particularly unusual. Weight losses of 2.2–5.9% in *B. c. interior* in southern Illinois have been recorded (Hanson 1962a, Raveling 1968). Adult Giant Canada Geese at Rochester, Minnesota lost 9.7–16.7% of their weight between November and February (M. L. Wege and Raveling, unpublished data). The large depletion of lipids in Cackling Geese (Tables 1 and 2) was, however, much different than the pattern for the other races. Lipid content of *B. c. interior* was not quantified, but the thinnest geese examined in winter had evident subcutaneous and abdominal fat deposits (Raveling 1968). The lipid content of Giant Canadas at their minimum winter weight, after a relatively greater weight loss than that of Cackling Geese, was 14.2% and 17.6% for males and females, respectively (M. R. McLandress and Raveling, unpublished data) or 2.8–3.7 times greater than in Cackling Geese.

Cackling Geese are much smaller than *B. c. interior* and *B. c. maxima* and they spend the winter in a much more moderate climate (see Hanson 1965, LeFebvre and Raveling 1967, and Raveling et al. 1972 for the other races). Cackling Geese also undertake extensive daily flights to reach their rice and grass food supplies. Much less flight activity is undertaken by the other races to obtain their staple winter food of corn. It is possible that there is a nutritional “deficiency” that inhibits the maintenance or deposition of fat in winter by Cackling Geese. I suggest, however, that because Cackling Geese did not exhibit greater relative weight losses than Giant Canadas, and lost little more than *B. c. interior*, the different patterns reflect basic differences in adaptations. The heavy subcutaneous fat deposits retained by the large Canada Geese serve two important functions: insulation during cold periods, and high energy nutrient reserves that enable the birds to survive periods of food shortage due to snow or cold weather during which the geese do not fly out even to attempt to gather food (Raveling et al. 1972). In contrast, Cackling Geese would rarely, if ever, encounter snow and cold weather sufficient to hamper their food gathering activities. The maintenance of the muscle masses and lack of extra weight stored as fat in Cackling Geese appear to be adaptations to their more extensive flying requirement, as probably is their smaller body size but relatively greater wing size (Table 9; the larger geese are 2.7–3.2 times heavier than *B. c. minima*, but have wings only 1.3 times as long).

While body size–metabolic rate relationships alone suggest that size is important in affecting distribution of Canada Geese in winter in accordance with Bergmann’s Rule (LeFebvre and Raveling 1967), the difference in fat storage may be the most important factor preventing the smaller Canadas from wintering farther north. Differences in physiological control of fat storage in relation to the ease of obtaining

food from the environment, and the frequency with which food shortages may occur in harsh climates, may account for the body size–distribution relationships for many species that conform to Bergmann's Rule (also see Calder 1974).

Spring weight gain.—The Cackling Goose leaves its wintering grounds before it has gained much weight or maximum reserves, as do other races of Canada Geese (Hanson 1962a, Raveling 1968). It is likely that their maximum weight is attained within a 2-week period prior to their departure from their last spring staging area, so that the geese arrive on nesting areas with maximum reserves that have been depleted only by the cost of the final migration flight. This cost is a small portion of the accumulated energy reserve (Raveling and Lumsden 1977). As food may be unavailable or scarce and of low quality when the geese arrive on the breeding grounds, these reserves are essential for the establishment of the territory, the production of eggs, and for the incubation fasting period for females. Females gained 1.8 times more weight, 2.4 times more fat, and 1.4 times more protein than did males, expressed as relative percentage increases over levels in early April.

Egg laying and incubation.—During the 17 days preceding incubation, both sexes lost an amount of weight nearly equivalent to that gained just before their arrival on the nesting grounds, as predicted in the model of Raveling and Lumsden (1977) (341 g in males and 503 g in females). High levels of mutual pair displays (Triumph Ceremony; Fischer 1965, Raveling 1970) and aggression are obvious until egg laying commences, at which time pairs become quiet and more secretive. Males used all their lipid reserves before incubation began, but protein stores, especially in the major muscle masses of breast and legs, remained higher than during winter until after hatching. During incubation, the males assume most of the territorial related behavior, which includes chases of jaegers (*Stercorarius parasiticus* and *S. longicaudus*) and tolling of foxes (*Vulpes fulva* and *Alopex lagopus*), as well as less frequent encounters with conspecifics. Females, however, did not lose all of their fat by the time of incubation onset as stated by Hanson (1962a: 33). Sufficient lipid stores remained in females to allow for their nearly constant incubation for the next 26 days, during which they lost an additional 292 g of their body weight and 138 g of lipids. Weight of males did not change significantly during the incubation period. Food supplies in the form of new growth of sedges and grasses became progressively more abundant during the time of egg laying and incubation, and males were obviously able to take advantage of this food.

Molt.—Geese leave their nest as soon as their newly-hatched goslings are dry. Walking, running, and swimming are the major means of travel and escape for adults as well as young and, of course, their sole methods when they become flightless. Correlated with this activity is an amazing hypertrophy of leg muscles (an increase of 92.6% in males and 100% in females from the winter low) and atrophy of breast muscles (a decrease of 45.9% in males and 41.9% in females from spring peaks). The pattern, however, varies between sexes. Leg muscles of males increased throughout the spring and summer, not just after the hatch as suggested by Hanson (1962a: 22), while the major decline (35.5%) of their breast muscles occurred after the incubation period. Breast muscles of females, however, declined 18.6% during incubation and a further 14.3% to the early molt stage, and leg muscles increased only after hatching.

The value of hypertrophy of leg muscles to aid in locomotion seems obvious, but the adaptiveness of the atrophy of the breast muscles is more obscure. Hanson (1962a: 31–37) concluded that Canada Geese reached their minimum weight during

molt and that the temporarily inactive flight muscles were drawn upon to provide sulfur-bearing amino acids necessary for feather growth during molt because geese were unable to consume sufficient food to meet the demands of feather synthesis. Hanson subsequently realized that hypertrophy of leg muscles began well before the onset of molt, and he then suggested that amino acids for this hypertrophy were partially derived from breast muscles (Hanson and Jones 1976: 192). Both explanations probably have some validity, but the phenomenon is mainly in males (Tables 3, 4), as total weight, lipid, and protein content of females (Table 2) increased after hatching, even though breast muscles did decline further (Table 5). Therefore, food supplies had to be sufficient to enable females not only to regain body weight, but to supply most of the needs for feather growth. Hanson's (1962a) explanation may still be valid, however. While not quantified, it is obvious that females feed voraciously and nearly constantly with their broods, whereas males remain more alert to disturbances and predators (also see Ankney 1977a, Lazarus and Inglis 1978). The reserves in females are exhausted during incubation, while the male has opportunity to feed. After hatching, the female is obligated to spend her time feeding because of her emaciated condition, while the male maintains body weight and total protein content (Table 1) while large shifts among protein pools are occurring (Tables 3, 4) (Ankney 1977a).

Hanson (1962a: 13–14) further stated that the stress of molting is particularly heavy on females following the demands of egg laying and that this stress may be a primary reason for the preponderance of males in adult waterfowl populations. This conclusion was apparently based on the appearance of the breast muscles, but as judged by total body weight, lipid, and protein stores, the most stressful period for females is during late incubation. There is doubt as to whether mortality of adult females exceeds that of males in Canada Geese (Imber 1968), and predation during incubation is likely a major cause of unbalanced sex ratios in ducks (Johnson and Sargeant 1977).

FAT METABOLISM

Hanson (1962a: 29) stated that superficial fat under the skin was metabolized before remnant visceral fat during incubation. Male Cackling Geese, however, had only trace amounts or no visible abdominal fat at the onset of incubation, but three of the five males collected at this time contained a continuous, 1–3-mm-thick, subcutaneous fat layer. The other two males had only trace amounts of subcutaneous fat and no abdominal fat. Females began incubation with a continuous, 2–8-mm-thick, subcutaneous fat layer and discontinuous, 3–4-mm-thick, fat deposits interspersed among the intestinal mesenteries. By mid-incubation, the subcutaneous fat layer was 1–5 mm thick, and only scattered 2–3-mm-thick deposits were present among the intestines. By the end of incubation, only trace amounts of subcutaneous fat, less than 1 mm thick in discontinuous patches, and no visible abdominal fat were present in six females. The other three females contained a few 1–3-mm patches of mesenteric fat and a nearly continuous, 1–3-mm-thick, subcutaneous layer. Thus, abdominal and subcutaneous fat were used simultaneously, but subcutaneous deposits were the last to be depleted. Maintenance of a continuous subcutaneous fat layer for as long as possible would seem to be advantageous in providing insulation, especially for the immobile, incubating female but also for the relatively inactive male. Ambient temperatures may commonly approach the freezing point, especially during early incubation.

Based on the appearance of starving geese and those in molt, Hanson (1962a: 24–26, 38–39) concluded that, in the absence of carbohydrates, a breakdown of tissue protein was necessary to supply the oxaloacetate necessary for metabolism of stored fats. There is a continuous turnover of tissue protein (Swick and Benevenga 1977), and thus it is certain that there is some loss of essential amino acids, which cannot be synthesized if the animal is either fasting or receiving an inadequate diet. However, oxaloacetate is continuously recycled, and Hanson's conclusion seems to over-emphasize the process and magnitude of protein loss that accompanies fat mobilization. The protein loss in females during the pre-nesting period occurred at the time of egg formation, and there was only a small loss in males during this time when nearly all their fat was used. During the fast of incubation, the loss of fat in females was virtually total in the body and breast muscles before protein levels declined. Although breast muscles of both sexes declined significantly in weight and protein content during the molt (Tables 3, 5) while total lipids increased (as observed by Hanson 1962a), the total protein content of the carcass of females increased (Table 2) and there was not a significant overall decline in males (Table 1). Thus, it is evident that deposition of protein is a highly complex process wherein tissues may differentially gain or lose nitrogen depending upon the comparative survival values of different organs at specific times of the annual cycle. The data do not support Hanson's (1962a) conclusion that a large tissue protein breakdown is necessary to mobilize fat.

CONTROL OF CLUTCH SIZE

The timing and synchrony of egg laying by geese results in synchrony of hatching of the young with an abundant new growth of food and maximizes the time available for young to develop and adults to molt before migration is necessitated in autumn (Cooch 1961, Barry 1962, Hanson 1962a, Harwood 1977, Raveling 1978). The modal clutch size results in absolutely and relatively the most goslings produced (Ryder 1972, Raveling and Lumsden 1977). Within a season, clutches initiated later are smaller than earlier ones, and clutches in late spring seasons are smaller than those in early seasons (Cooch 1961; Barry 1962; Ryder 1967, 1972; Raveling and Lumsden 1977). Most authors have stressed that reduced clutches are adaptive because they speed up the cycle of events critical for arctic migratory species. I doubt, however, whether the one or two days saved is that critical.

Barry (1962) concluded that resorption of ovarian follicles was necessitated by a lack of food necessary to sustain Atlantic Brant (*Branta bernicla hrota*) when there were delays to nesting. Ryder (1970) suggested that the amount of reserves allocated to eggs varied in different-sized clutches, but Ankney and Bisset (1976) did not find this to be true in Lesser Snow Geese. Except for Barry's (1962) suggestion, proposed explanations had teleological implications of anticipation by the goose. The question is: what is the proximate mechanism that results in cessation of egg laying at the appropriate time? Raveling and Lumsden (1977) proposed that it was the depletion of the accumulated energy store of the female after maximum reserves had been allotted to eggs, and that this level approximated the "basal" winter weight level. Ankney and MacInnes (1978) suggested that clutch size of Lesser Snow Geese was determined by the size of stored nutrient reserves.

The ice- and snow-melt in spring 1974 was unusually early, but Cackling Geese

arrived at their "usual" time in mid-May and laid large clutches as soon as they were physiologically capable of doing so (Raveling 1978). Thus, the peak weight accumulation observed in these birds should represent the optimum. Body weight, lipid, and protein levels of females after egg laying were essentially equal to October and April levels, suggesting that egg laying ceased when some essential material(s) accumulated just prior to arrival on the nesting area was depleted.

Ether extraction and Kjeldahl nitrogen analysis of one egg revealed its contents to be 12.7% lipid and 14.8% protein (as % of fresh weight). The average weight of a fresh egg was 97 g (N = 138). Therefore, an average clutch of five represented the mobilization of 72 g of protein and 62 g of lipid from the body stores of the female. Therefore, most of the lipids lost between arrival and the onset of incubation (361 g) were used as energy for maintenance; however, the loss of protein (80 g) was nearly equal to that incorporated into eggs. Much of the registered "protein" losses were, however, minerals for egg shells (44 g). Thus, it appears that the peak protein content of pre-laying females was slightly underestimated, or that dietary intake during egg formation was an important source of amino acids for egg protein. Food becomes steadily more available after geese arrive on nesting areas, and females especially attempt to feed during the egg-laying period while males remain alert. I interpret the data as support for the suggestion that the mechanism of cessation of egg laying involves depletion of protein reserve, as concluded for Red-billed Queleas by Jones and Ward (1976).

Korschgen (1977) pointed out that weight loss from the gizzard was almost all protein and would fulfill 38% of the protein requirements of the clutch of Common Eiders and that similar, but smaller, decreases in pectoral muscles and intestines probably contribute much of the rest of the requirement for the clutch. In female Cackling Geese, the gizzard lost 23 g, which would equal about 6 g of protein (at 73% water, see Korschgen 1977). Breast muscle protein declined 18.6 g, and liver protein decreased 7.5 g. Thus, the loss of protein from these three tissues (32.1 g) is equal to about 45% of the protein content of an average clutch. Intestines were not weighed, but their total length (large and small intestines) declined 473 mm (26.3%) between the time of their arrival and onset of incubation in females (see also Ankney 1977b).

The probable shifts of protein to eggs from organs of digestion and pectoral muscles seem highly adaptive. The gut and flight muscles are used little during incubation, but they hypertrophied during the period of maximum weight gain immediately prior to arrival and nesting. The loss of weight of these organs, which do not have a major function during fasting, would lower the cost of supporting these metabolically active tissues.

The fact that males also exhibited marked declines in liver protein (5.3 g), gizzard weight (14 g or about 4 g of protein), and gut length (416 mm, 18.4%) indicates that not all of these losses provide a protein pool for eggs. However, the relatively greater increase, and then loss, in these tissues of females suggests that they are important sources for egg protein. Korschgen (1977) and Ankney (1977b) concluded that loss of weight of intestines and gizzard represented adaptations caused by other than disuse phenomena.

Another factor that could be limiting clutch size is shell material, particularly calcium. Because calcium content, cortical weights, and ash of tibiotarsi and femurs of Cackling Geese were higher at the onset of incubation than during the non-breeding season, Raveling et al. (1978) concluded that calcium deficiency was prob-

ably not a major factor in clutch limitation, but the contribution from other bones (cf. Taylor and Moore 1954) needs investigation.

It seems clear that we have reached the point where clarification of the exact nature of what reserves are limiting for formation of eggs, and from what tissues these materials are mobilized, will require use of labeled compounds. Bartholomew (in Paynter 1974) succinctly pointed out that future insights into reproductive evolutionary strategies will depend upon quantitative biochemical investigations.

Consequences of clutch limitation.—Regardless of what factor(s) limits egg laying when geese reach their "basal" weight level, the mechanism is essential and highly adaptive. The laying of one or two more eggs beyond the point at which they now cease laying would result in females beginning incubation at a 100–200 g lighter body weight, with further reduced lipid and protein stores (plus the additional cost of maintenance during the time required to lay those eggs). An incubating female with severely depleted body stores would either starve on the nest [which has been recorded for Lesser Snow Geese by Harvey (1971) and Ankney and MacInnes (1978)] or have to leave the nest more frequently and for longer periods to feed. Geese that are less attentive incubators lose their clutches to predators at a higher rate than do attentive females (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977). Therefore, the control of egg laying involves a mechanism of cessation that allows females to devote maximum energy to eggs while retaining sufficient reserves to incubate nearly continuously.

The dependence of the clutch size on stored reserves in the body demonstrates that the peak spring weight accumulation is critical in determining the potential for egg laying. Therefore, variation in food supply or storage during spring migration could cause annual variation in clutch size, as suggested by MacInnes et al. (1974) and Ankney and MacInnes (1978). When the interval between arrival and egg laying is delayed, clutch sizes would decline in proportion to amounts of stored reserves used for maintenance instead of egg formation. The costs of delayed springs in terms of reduced clutches are greatest in the smaller geese, which have a higher metabolic rate in relation to body mass and lay eggs that are a larger proportion of their body weight than do larger forms (Raveling and Lumsden 1977).

Johnsgard (1973) argued that increased probability of predation on nests during laying, coupled with decreasing optimum available breeding time and parental effectiveness, were more important factors selecting for optimum clutch size in geese and swans than Lack's (1967, 1968a) general explanation of limited food supply during laying. Available data do not support the suggestion that predation on eggs is an important proximate factor in geese (Raveling and Lumsden 1977). The carcass composition data presented here and by Ankney and MacInnes (1978) demonstrate the critical relationship between stored reserves and clutch potential and support Ryder's (1970) extension of Lack's (1967, 1968a) proposal, as refined here and in Raveling and Lumsden (1977).

Comparative strategies.—It is clear that Common Eiders undergo weight changes during egg laying and their constant incubation very similar to geese (Milne 1976, Korschgen 1977). The major difference between geese and most other ducks is that energy for egg laying by ducks is gathered after arrival on nesting areas in synchrony with blooms of abundance of different high protein invertebrate food items (Swanson and Meyer 1973; Swanson et al. 1974; Krapu 1974a, b; Serie and Swanson 1976). With the exception of the eider studies, collections of ducks at precisely known points in the egg-laying or incubation cycle have been difficult to attain. However,

it is clear that their body weights are greatly reduced by the end of egg laying and that incubating birds become thin (see also Harris 1970). Depletion of body stores in ducks can be compensated for by feeding during their longer and more frequent incubation breaks (Low 1945, Breckenridge 1956, Caldwell and Cornwell 1975, Miller 1976) as compared to geese. These incubation breaks are presumably permissible in terms of predation because of nest concealment and reneating potential. Reneating in ducks is possible because their smaller body size and shorter time required for growth of young and completion of molt in relation to the length of time that food supplies are available allow them to regain the reserves needed for egg laying and incubation. Clutch size varies in relation to food supply (Bengston 1971). These patterns strongly support Lack's (1967, 1968a) explanations for the evolution of reproductive rates in waterfowl and precocial species.

ACKNOWLEDGMENTS

This study was financed in part by a faculty research grant from the College of Agriculture, University of California, Davis, and by the U.S. Fish and Wildlife Service, which supplied logistic support, supplies, and equipment. I am grateful to C. J. Lensink, J. Hout, J. Paniyak, C. Dau, R. Watson, E. O'Neill, and E. Collins of the U.S. Fish and Wildlife Service, and W. Rienecker, D. Hinz, and F. Kozlik of the California Department of Fish and Game for their cooperation and assistance in the field. Assistance in collecting geese and processing carcasses was provided by many students, especially M. R. Petersen, M. L. Wege, and M. R. McLandress. The Animal Science Department of the University of California, Davis, generously made available the expert advice of J. Bryan and N. Hinman and the equipment needed for lipid determinations. N. K. Jacobsen provided constructive criticism of the manuscript.

LITERATURE CITED

- 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.
- , & A. R. BISSET. 1976. An explanation of egg-weight variation in the Lesser Snow Goose. *J. Wildl. Mgmt.* 40: 729-734.
- , & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. *J. Wildl. Mgmt.* 26: 19-26.
- BENGSTON, S. A. 1971. Variations in clutch size in ducks in relation to food supply. *Ibis* 113: 523-526.
- BRECKENRIDGE, W. J. 1956. Nesting study of Wood Ducks. *J. Wildl. Mgmt.* 20: 16-21.
- CALDER, W. A., III. 1974. Consequences of body size for avian energetics. Pp. 86-144 in *Avian energetics* (R. A. Paynter, Ed.). Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club No. 15.
- CALDWELL, P. J., & G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard Duck. *Auk* 92: 706-731.
- COOCH, F. G. 1961. Ecological aspects of the Blue-Snow Goose complex. *Auk* 78: 72-89.
- FISCHER, H. 1965. Das Triumphgeschrei der Graugans (*Anser anser*). *Z. Tierpsychol.* 22: 247-304.
- FISHER, H. I., & L. M. BARTLETT. 1957. Diurnal cycles in liver weights in birds. *Condor* 59: 364-372.
- HANSON, H. C. 1962a. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arctic Inst. N. Amer. Tech. Paper No. 12*.
- . 1962b. Characters of age, sex, and sexual maturity in Canada Geese. III. *Nat. Hist. Surv. Biol. Notes* 49.
- . 1965. *The Giant Canada Goose*. Carbondale, Illinois, S. Ill. Univ. Press.
- , & R. L. JONES. 1976. *The biogeochemistry of Blue, Snow and Ross' Geese*. III. *Nat. Hist. Surv. Spec. Publ. No. 1*. Carbondale, Illinois, S. Ill. Univ. Press.
- HARRIS, H. J. 1970. Evidence of stress response in Blue-winged Teal. *J. Wildl. Mgmt.* 34: 747-755.
- HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. *Can. J. Zool.* 49: 223-234.
- HARWOOD, J. 1977. Summer feeding ecology of Lesser Snow Geese. *J. Wildl. Mgmt.* 41: 48-55.
- IMBER, M. J. 1968. Sex ratios in Canada Goose populations. *J. Wildl. Mgmt.* 32: 905-920.

- INGLIS, I. R. 1977. The breeding behaviour of the Pink-footed Goose: Behavioural correlates of nesting success. *Anim. Behav.* 25: 747-764.
- JOHNSGARD, P. A. 1973. Proximate and ultimate determinants of clutch size in Anatidae. *Wildfowl* 24: 144-149.
- JOHNSON, D. H., & A. B. SARGEANT. 1977. Impact of red fox predation on the sex ratio of prairie Mallards. U.S. Dept. Int. Fish Wildl. Serv. Wildl. Res. Rept. 6.
- JONES, P. J., & P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea *Quelea quelea*. *Ibis* 118: 547-574.
- KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78-107 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Nat. Acad. Sci.
- . 1974. Seasonal allocation of time and energy resources in birds. Pp. 4-85 in *Avian energetics* (R. A. Paynter, Jr. Ed.). Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club No. 15.
- KORSCHGEN, C. E. 1977. Breeding stress of female eiders in Maine. *J. Wildl. Mgmt.* 41: 360-373.
- KRAPU, G. L. 1974a. Feeding ecology of Pintail hens during reproduction. *Auk* 91: 278-290.
- . 1974b. Foods of breeding Pintails in North Dakota. *J. Wildl. Mgmt.* 38: 408-417.
- LACK, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 18: 125-128.
- . 1968a. Ecological adaptations for breeding in birds. London, Methuen.
- . 1968b. The proportion of yolk in the eggs of waterfowl. *Wildfowl* 19: 67-69.
- LAZARUS, J., & I. R. INGLIS. 1978. The breeding behaviour of the Pink-footed Goose: Parental care and vigilant behaviour during the fledging period. *Behaviour* 45: 62-87.
- LEFEBVRE, E. A., & D. G. RAVELING. 1967. Distribution of Canada Geese in winter as related to heat loss at varying environmental temperatures. *J. Wildl. Mgmt.* 31: 538-546.
- LOW, J. B. 1945. Ecology and management of the Redhead, *Nyroca americana*, in Iowa. *Ecol. Monogr.* 15: 35-69.
- 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.
- MICKELSON, P. G. 1975. Breeding biology of Cackling Geese and associated species on the Yukon-Kuskokwim Delta, Alaska. *Wildl. Monogr.* No. 45.
- MILLER, K. J. 1976. Activity patterns, vocalizations, and nest site selection in nesting Blue-winged Teal. *Wildfowl* 27: 33-43.
- MILNE, H. 1976. Bodyweights and carcass composition of the Common Eider. *Wildfowl* 27: 115-122.
- NELSON, U. C., & H. A. HANSEN. 1959. The Cackling Goose—its migration and management. N. Amer. Wildl. Nat. Resour. Conf. Trans. 24: 174-186.
- PAYNTER, R. A., JR. (ED.). 1974. *Avian energetics*. Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club No. 15.
- RAVELING, D. G. 1968. Weights of *Branta canadensis interior* during winter. *J. Wildl. Mgmt.* 32: 412-414.
- . 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. *Behaviour* 37: 291-319.
- . 1978. The timing of egg laying by northern geese. *Auk* 95: 294-303.
- , W. E. CREWS, & W. D. KLIMSTRA. 1972. Activity patterns of Canada geese in winter. *Wilson Bull.* 84: 278-295.
- , & H. G. LUMSDEN. 1977. Nesting ecology of Canada Geese in the Hudson Bay Lowlands of Ontario: Evolution and population regulation. Ontario Ministry Nat. Resources. Fish and Wildlife Res. Rept. No. 98.
- , M. SIFRI, & R. B. KNUDSEN. 1978. Seasonal variation of femur and tibiotarsus constituents of Canada geese. *Condor* 80: 246-248.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292 in *Avian energetics* (R. A. Paynter, Jr., Ed.). Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club No. 15.
- RYDER, J. P. 1967. The breeding biology of Ross' Goose in the Perry River region, Northwest Territories. *Can. Wildl. Serv. Rept. Ser. No.* 3.
- . 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82: 5-13.
- . 1972. Biology of nesting Ross's Geese. *Ardea* 60: 185-215.
- SERIE, J. R., & G. A. SWANSON. 1976. Feeding ecology of breeding Gadwalls on saline wetlands. *J. Wildl. Mgmt.* 40: 69-81.
- SOKAL, R. R., & F. J. ROHLF. 1969. *Biometry*. San Francisco, California, W. H. Freeman.
- SWANSON, G. A., & M. I. MEYER. 1973. The role of invertebrates in the feeding ecology of Anatinae

- during the breeding season. Pp. 143-185 *in* Waterfowl habitat management symposium. Moncton, New Brunswick, Atlantic Waterfowl Council.
- , ———, & J. R. SERIE. 1974. Feeding ecology of breeding Blue-winged Teals. *J. Wildl. Mgmt.* 38: 396-407.
- SWICK, R. W., & N. J. BENEVENGA. 1977. Labile protein reserves and protein turnover. *J. Dairy Sci.* 60: 505-515.
- TAYLOR, T. G., & J. H. MOORE. 1954. Skeletal depletion in hens laying on a low calcium diet. *Brit. J. Nutr.* 8: 112-124.
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