

CHANGES IN DIET AND BODY COMPOSITION OF CANADA GEESE BEFORE SPRING MIGRATION

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ABSTRACT.—Changes in diet and body composition of Giant Canada Geese (*Branta canadensis maxima*) were studied before geese initiated spring migration in early April. During the period of hyperphagia in March, body weight of female and male geese increased 36% and 26%, respectively, above average winter weights. Body weights of paired geese averaged 0.34 kg (females) and 0.27 kg (males) more than those of geese without mates before the weight gain period. Some unmated geese did not gain weight, and others gained less weight than paired geese.

Geese shifted from a winter diet of corn (*Zea mays*) to a diversity of food items in spring. Corn remained the primary source of carbohydrate, and bluegrass (*Poa pratensis*) provided protein for geese. Weight gain of females was composed of 61% lipid, 10% protein, and 21% water, whereas weight gained by males was 47% lipid, 13% protein, and 35% water. Initial weight gains were predominantly protein (and accompanying water), probably required for gut enlargement. Most of the later body weight gain was due to lipid storage. Increase in size of breast and leg muscles at the end of March was largely due to lipid storage and a shift of protein from other body tissues. Lipid and protein storage was adequate to explain energy and nutrient requirements for body maintenance after arrival on the breeding grounds, egg laying, and territorial defense. Females may have to obtain minerals (and possibly additional protein) for egg formation from food sources on the breeding grounds. Lipid reserves of male Giant Canada Geese indicate an ability to sustain energetic costs during nesting equal to those of the female (apart from egg laying) and are greater than reserves of other species of geese and subspecies of Canada Geese investigated to date.

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THE importance of lipid and protein reserves for reproduction by geese has been the subject of much recent discussion (Ankney 1977; Raveling and Lumsden 1977; Ankney and MacInnes 1978; Raveling 1978a, 1979a, b). Increases in body weight of females in spring of 41–53% of winter weight have been documented for Todd's Canada Goose (*Branta canadensis interior*, Hanson 1962a), Ross' Goose (*Chen rossii*, Ryder 1967), Lesser Snow Goose (*Chen caerulescens caerulescens*; Ankney 1977, Ankney and MacInnes 1978), and the Cackling Goose (*B. c. minima*, Raveling 1979a). These reserves provide the necessary energy for migration and reproduction and are critical in affecting clutch size. The evolutionary and functional significance of these weight gains was discussed in the papers cited above (see also Barry 1962, Ryder 1970). Few data exist on the process of acquisition of maximum body weights by geese during spring, however, and most previous studies used qualitative measures or indirect indices of body composition of free-living geese (Hanson 1962a, Ryder 1970, Ankney 1977, Ankney and MacInnes 1978, Wypkema and Ankney 1979). Recently, body components were quantified and energetic strategies discussed for Common Eiders (*Somateria mollissima*, Korschgen 1977) and Cackling Geese (Raveling 1979a, b). The purpose of this study was to use similar methods to measure quantitatively the changes in body constituents and skeletal muscles undergone by adult Giant Canada Geese (*B. c. maxima*, Hanson 1965). We related these changes to food habits, social status, and timing of spring migration in order to understand better the behavior attendant to and the factors controlling the attainment of the annual reproductive state.

METHODS

Giant Canada Geese wintering at Silver Lake in Rochester, Minnesota (43°55'N, 92°30'W) were studied between 3 February and 6 April 1974. This population nests in Canada between Lakes Winnipeg and Manitoba-Winnipegosis, 885 km northwest of Rochester (Gulden and Johnson 1968; Raveling 1976a, b, 1978b). Geese migrate to the nesting grounds during the first or second week of April (mass departures on 2 and 6 April during this study).

Over 200 individually identifiable neck-banded adult geese were available for observation. Family status of geese was determined from behavioral associations (see Raveling 1969), especially the Triumph Ceremony (Fischer 1965). This display involves extensive head and neck movements with associated vocalizations and is usually exhibited only by mated pairs of adults and among members of a family.

Food habits and specimen collection.—Thirty-three adult geese were shot at feeding areas in the vicinity of Rochester. Collections were intentionally biased towards birds with mates. Geese were collected in four different time periods: 12–16 February, 4–7 March, 14–16 March, and 4–6 April. Esophageal contents were removed from the birds within 5 min of their death (with the exception of one bird, which was not found immediately) to enable identification of any invertebrates ingested (Swanson and Bartonek 1970). These contents, as well as samples of food items collected at sites where geese were observed feeding, were frozen immediately. Later, food samples were oven-dried at 70°C, and a Goldfish apparatus was used for ether extraction of lipids. The lipid-free residue was used for determination of acid detergent fiber. Nitrogen was determined by Kjeldahl procedure and ash by 12 h of combustion in a muffle furnace at 575°C.

Analysis of specimens.—After esophageal contents were removed, adult geese were frozen and transported to the University of California, Davis. Each specimen was then thawed and analyzed following procedures detailed by Raveling (1979a), except for different treatment of the ovary. In summary, water and lipid content was determined by freeze-drying followed by ether extraction of a 100-g sample of the right breast muscle and two 100-g samples of a homogenate of remaining parts of the carcass. Component parts were proportioned to yield total body water and lipid content, although ovaries and one of the femurs, tibiotarsi, and humeri were removed before carcass analysis. Protein content was not measured directly but was determined by subtraction. Thus, the use of protein herein refers to the weight of dry, non-ether extractible residue, which also includes minerals (see Raveling 1979a).

Data for body composition and organ changes of 31 adult geese are presented. Two adult females were excluded from most analyses. One was not found until 2 days after shooting, and internal organs had begun to decompose. The other weighed 913 g less than the average of other geese collected at the time and had enlarged adrenal glands, which indicated that inclusion of this bird would bias the representation of "normal."

Body weights.—Body weights of 319 trapped and collected geese [203 adults, 30 yearlings (birds between 1 and 2 yr old) and 86 immatures] were measured to ± 10 g on a Chatillon spring scale. Nine marked adults and one marked yearling were recaptured and weighed more than once during spring. Some of the geese were held in captivity for 3–5 days and fitted with radio transmitters for migration study (Wege 1979). Criteria for recognition of age classes were presented by Hanson (1962b). Geese were trapped at Silver Lake with cannon nets or by luring specific marked individuals with bait (corn) close enough to be caught by hand. Some geese at Silver Lake become habituated to people and allow close approach (Gulden and Johnson 1968, Raveling 1978b).

One-way and two-way analysis of variance tests were used to determine differences in body weights and skeletal muscle weights between collection periods and sexes (Sokal and Rohlf 1973). Tests for significance in regression analysis of all measurements with time were conducted. Correlation coefficients were calculated (Sokal and Rohlf 1973: 271) for comparisons of body and muscle components.

RESULTS AND DISCUSSION

Details of feeding behavior in relation to location, weather, and agonistic and sexual interactions are to be the subject of another report (McLandress and Raveling, unpublished). Briefly, these findings included: (1) geese fed on grass as soon as it was exposed by melting snow; (2) time spent feeding increased markedly with warm temperatures and increased food availability, which began on 1 March; and (3) paired female geese spent more time feeding than males and more time than females without mates.

TABLE 1. Percent occurrence of food items in the esophagi, proventriculi, and gizzards of adult Giant Canada Geese collected during spring 1974.

Food items	Dates of collection				Total
	12-16 February	4-7 March	14-16 March	4-6 April	
Number of geese collected	8	9	8	8	33
Percentage with:					
Corn	50	78	63	13	52
Bluegrass	13	44	13	75	36
Roots (unidentified spp.)	25	22	38	25	27
Spike rush		11	38	13	15
Plant remains (green)	13		13	25	12
Bulrush tubers		11	13	25	12
Millet seeds			13	13	6
Cereal grains		11			3
Duckweed			13		3
Snails				13	3
No food items present	38				9

FOOD HABITS

Corn (*Zea mays*) and grass, almost exclusively stems of bluegrass (*Poa pratensis*), were the most common food items consumed (Table 1). Root parts of unidentified plants and spike rush (*Eleocharis* sp.; entire plants) were also common. Less commonly used foods were bulrush tubers (*Scirpus* sp.), duckweed (*Lemna* sp.), and grass seeds of the millet tribe (*Panicaceae*). Mud was present with corn or roots in esophageal contents of geese during March. Snail shells (Class: Gastropoda) were found in a female goose that had an egg in its oviduct. This goose, excluded from analysis due to tissue decomposition, was probably one of a small group (<100 of 20,000+) of birds that nest near Rochester.

Grass.—Crude protein of bluegrass from esophagus samples was the highest (26.2%) of any food item (Table 2). Grass gathered from beneath the snow in February contained approximately 50% dead material. An analyzed sample of dead grass contained only 5.5% crude protein. Subnivean living grass must have contained more than 30% crude protein to offset the low protein content of dead grass in the mixed sample (18.2% protein, Table 2).

Bluegrass is a good source of essential amino acids (Livingston et al. 1971). According to McDonald et al. (1973), grasses are rich in glutamine and asparagine (which are necessary for protein synthesis), unsaturated fatty acids, and carotene (a precursor to Vitamin A). Grass is not a good source of linoleic acid (an essential fatty acid that is abundant in corn) or some minerals, most notably calcium (McDonald et al. 1973).

It was likely that geese selected bluegrass during spring, although we did not determine availability of alternate species. Of 269 blades of bluegrass removed from collected geese, 81% were "narrow" (≤ 4 mm). Lengths of "broad" pieces of the same species of grass (> 4 mm) were longer ($\bar{x} = 40.3 \pm 3.4$ mm SE) than lengths of "narrow" pieces ($\bar{x} = 21.2 \pm 0.8$ mm, $t = 8.02$, $P < 0.001$). The leaf tip was intact on 61% of grass blades. Therefore, geese tended to clip grass at a consistent level just above the ground rather than taking a specific length of grass blade. As cell enlargement is due largely to the uptake of water (Galston 1964), the highest concentration of nutrients (largely protein) in a young grass stem is in the cell differ-

TABLE 2. Composition of major food items used by Giant Canada Geese during spring.

Food item	Percentage water in food item	Constituents (expressed as g per 100 g of dry matter) ^a				
		Crude protein	Lipid	Fiber	Ash content	Other ^b
Corn						
February (p; n = 2) ^c	19.3 ^d (19.2-19.4)	11.6 (11.5-11.6)	4.2 (4.2-4.2)	2.9 (2.9-2.9)	1.7 (1.7-1.7)	79.6
March (p; n = 3)	40.1 (31.0-46.6)	10.4 (9.6-11.1)	4.3 (4.2-4.3)	2.8 (2.5-3.2)	1.5 (1.3-1.6)	81.0
March (t; n = 4)	41.8 (37.8-45.4)	10.0 (9.1-10.8)	4.1 (4.0-4.2)	3.7 (3.1-5.4)	2.4 (2.0-3.4)	79.8
Bluegrass						
February (sub-nival, p)	92.9	18.2 ^e	3.2	31.1	14.4	33.1
March (p)	72.1	22.7				
March (t)	94.1	26.2				
Roots (unident. spp., p)	88.0	3.9	3.1	26.0	56.1	10.9
Spike rush (t)	86.5	12.7	1.2	19.7		
Bulrush tubers (t)	66.9	7.4				
Millet seeds (t)						
<i>Setaria</i> sp.	51.2	9.1	1.7	12.6		
<i>Panicum</i> sp.	83.7	14.6				

^a Where no data are presented there was an insufficient quantity of a food item for complete analysis.

^b Largely carbohydrate, determined by subtraction.

^c Source of food item: p = gathered by investigator; t = esophageal contents of geese; n = sample size if greater than one.

^d Mean (range when n > 1).

^e Sample included only 50% new growth (see text).

entiation area of the intercalary meristem at the leaf base (Ray 1972). This meristem is at ground level in newly emerging grass. Narrow blades were no doubt younger than the wide pieces of bluegrass consumed. The highest levels of protein and lowest levels of indigestible cellulose and lignin are contained in young grass (McDonald et al. 1973). Thus, the method of grazing by Canada Geese provided maximum protein intake.

Other foods.—Corn remained an important food item for geese throughout the study. Corn gathered after the spring thaw contained twice as much water as winter corn, but levels of protein and lipids were essentially unchanged (Table 2). As with other cereal grains, corn is essentially a high energy carbohydrate concentrate. Carbohydrate may not be fully assimilated by wintering geese restricted to a diet of corn, however, because of inadequate dietary protein. Adult Canada geese lose weight during winter (Elder 1946, Hanson 1962a) regardless of food availability (Williams 1965, Raveling 1968). Corn protein lacks the essential amino acids of tryptophan, lysine, and an adequate amount of methionine (McDonald et al. 1973). Grass may provide proteins for enzymatic activity necessary for more complete conversion of cornstarch to fat in spring. Geese ate some grass seeds, bulrush tubers, and spike rush. These food items were probably more important carbohydrate sources before man's cultivation of corn.

Roots of unidentifiable plants had the lowest protein content but highest ash content of any food item (Table 2). This indicates that roots could provide geese with minerals. Mud ingested while feeding on corn may also supply minerals and/or microorganisms. The incidence of snail shells (a potential source of calcium) ingested by a female goose containing an egg in her oviduct suggests the need for further investigation of the timing and sources of mineral acquisition.

CHANGES IN BODY WEIGHT

Geese obtained small amounts of grass from snow-free areas at Silver Lake roosting areas in early February, but intensive feeding on grass began 17 February, when melting snow exposed grass at feeding sites. After this date, the mean (\pm SE) weight of adult females increased by 36% from 3.77 ± 0.06 kg on 23–27 February to 5.12 ± 0.09 kg between 4 and 6 April ($t = 8.27$, $P < 0.001$, Table 3). Regression analysis indicated that weight increased 36 g per day ($F_s = 166.67$, $P < 0.01$). There was no significant difference among mean body weights of female geese captured 7–16 February, 23–27 February, and 1 March ($F = 0.56$, $P > 0.50$). From 7 February to 1 March, the average weight of 27 adult female neck-banded geese observed with mates was 3.96 ± 0.06 kg. During the same period, 11 marked adult females without mates averaged only 3.62 ± 0.09 kg ($t = 3.24$, $P < 0.01$). Four marked adult females that had mates and were captured more than once over an 11–39-day span showed a weight gain ($\bar{x} = 35$ g per day, range = 17–50, Table 4) that corresponded to the gain of the sampled population of adult females. One marked female that was not seen with a mate (two observations) lost 310 g during a 17-day span at the time the sample population had gained 612 g.

Body weight of adult males increased 26% from 4.46 ± 0.06 kg on 23–27 February to 5.61 ± 0.18 kg on 4–6 April ($t = 6.30$, $P < 0.001$, Table 3). The rate of weight gain of adult males, 29 g per day ($F_s = 30.26$, $P < 0.01$), was significant but was not statistically different from the rate of female weight gain. No significant difference was found among samples of males weighed 16 February, 23–27 February, and 1 March ($F = 0.26$, $P > 0.75$). The average weight of paired adult males between 7 February and 1 March, was 4.57 ± 0.06 kg ($n = 32$), while the average weight of seven unpaired adult males was 4.30 ± 0.10 kg ($t = 1.96$, $P < 0.1$). Two marked males having mates and one of undetermined status that were recaptured (Table 4) had gained weight ($\bar{x} = 15$ g per day, range = 4–24), although the gain was of less magnitude than that of the population sample. One adult male known to be without a mate was captured on 10 February and again on 12 March. He had gained only 30 g (1 g per day).

MacInnes et al. (1974) suggested that amounts of energy reserves obtained during spring may vary depending upon the initial state of an individual. Low winter body weights and the slow premigratory weight gain of adult geese without mates could explain some smaller clutch sizes of geese. Grass remains highly digestible until ears emerge (approximately 1 month in spring), at which time digestibility decreases abruptly (McDonald et al. 1973). If pairing occurred late in spring and the quality of grass had declined or the length of time was too short to complete fattening, such geese could arrive on nesting grounds with less than maximum energy reserves. It follows that these newly formed pairs of geese might lay fewer eggs (or not nest at all).

The mean weight of 21 immature female geese captured 23–26 February (Table 5) was significantly less than the average weight of 31 adult females (Table 3) weighed during the same period ($t = 4.40$, $P < 0.0005$, one-tailed test). Similarly, 26 immature males captured then (Table 5) weighed less than 26 adult males (Table 3) caught during the same days ($t = 5.44$, $P < 0.0005$, one-tailed test). Immature female geese gained 33 g per day during the fattening period ($F_s = 31.21$, $P < 0.01$). This rate did not differ significantly from the 36 g per day weight increase of

TABLE 3. Body weights (kg) of adult Canada Geese before spring migration.

Status and sex	Dates of capture						
	7-16 February	23-27 February	1 March	5-12 March	14-19 March	23-25 March	4-6 April
	All geese						
Males	4.53 ± 0.09 ^a n = 15	4.46 ± 0.06 n = 26	4.45 ± 0.09 n = 20	5.23 ± 0.10 n = 13	5.05 ± 0.11 n = 11	5.14 ± 0.10 n = 12	5.61 (5.43-5.79) n = 2
Females	3.85 ± 0.05 n = 33	3.77 ± 0.06 n = 31	3.85 ± 0.12 n = 11	4.31 ± 0.18 n = 8	4.54 ± 0.10 n = 9	4.76 ± 0.07 n = 7	5.12 ± 0.09 n = 5
	Geese of known status						
Paired							
Males	4.66 (4.09-5.09) n = 4	4.52 ± 0.09 n = 15	4.62 ± 0.10 n = 13	5.45 ± 0.18 n = 5		5.38 (5.02-5.74) n = 2	
Females	4.05 ± 0.06 n = 11	3.83 ± 0.10 n = 12	4.10 (3.83-4.31) n = 4	4.32 (3.94-4.69) n = 4	4.60 n = 1	4.74 (4.55-4.93) n = 2	
Single							
Males	4.74 n = 1	4.32 (4.22-4.42) n = 3	4.12 (3.84-4.33) n = 3	5.10 (4.70-5.44) n = 3		4.72 n = 1	
Females	3.63 (3.52-3.83) n = 3	3.59 ± 0.15 n = 5	3.66 (3.21-4.17) n = 3	3.75 n = 1			

^a Mean ± SE (range when n < 5).

TABLE 4. Body weights (kg) of marked Giant Canada Geese that were captured more than once during spring.

Age and Sex	Status	Weight (kg) on	
		First capture (date)	Second capture (date)
Adult male	Paired	4.65 (1 March)	5.27 (12 March) ^a
	Paired	5.68 (10 March)	5.74 (25 March)
	Single	4.74 (7 February) ^b	4.70 (12 March)
	Unknown	4.20 (1 March)	4.72 (23 March)
Yearling female	Paired	4.04 (24 February)	4.52 (23 March)
Adult female	Paired	4.30 (8 February) ^c	4.55 (23 March)
	Paired	3.97 (12 February) ^d	4.60 (19 March)
	Paired	3.58 (24 February)	4.38 (12 March)
	Paired	4.17 (1 March)	4.93 (24 March)
	Single	4.06 (23 February)	3.75 (12 March)

^a This bird was captured again on 23 March and weighed 5.02 kg.

^b Released 10 February (4.67 kg).

^c Released 12 February (3.90 kg).

^d Released 17 February (3.38 kg).

adult females. Too few immature male geese were weighed after 26 February to determine weight gain.

Only eight yearling males and 15 yearling females were weighed after 16 February (Table 5). Weights of males were highly variable, and no pattern was discerned. Weights of 11 yearling female geese were within the range of weights of adult females captured after 16 February. One of these, a marked bird, had a mate and weighed 4.04 kg on 24 February and 4.52 kg on 23 March (Table 4), indicating a gain of 18 g per day during that period. This was a smaller weight increase than that of three of the paired adult female geese weighed more than once. The remaining four yearling females captured on 24 and 25 February, three of which were neck collared, weighed less than any adult female. One of the marked geese of this group was seen several times following and displaying the Triumph Ceremony with a pair of marked adult geese, and a second was seen following a marked adult female. These adults were probably parents of the yearling geese, as yearlings commonly rejoined their families at Rochester (Raveling 1979c).

It is unlikely that either immature birds or small yearlings had attained the physiological development necessary for reproduction. Immature geese (1-yr-olds upon arrival on the nesting grounds) almost never nest, and yearlings (2-yr-olds on nesting grounds) often do not (see Bellrose 1976 for review). The larger yearlings (i.e. comparable in size to adult geese) may have been capable of reproduction. The below-average clutch size of nesting 2-yr-olds (Brakhage 1965) is probably a result of lower energy reserves being stored during the spring fattening period compared to adult geese, as also suggested by Raveling and Lumsden (1977), rather than of young geese using fewer body reserves for egg production, as suggested by Ryder (1970). In addition, because young geese nest later, they probably use more reserves for maintenance, thus further contributing to a smaller clutch size.

BODY COMPOSITION DYNAMICS

Carcass analysis.—Changes in body weights and weights of lipids, water, and lipid-free residue (protein) of collected adult geese are presented in Table 6. Body weights of geese collected just before the 6 April migration averaged 1,321 g (females) and 1,425 g (males) more than weights of birds collected 12–16 February. Lipid

TABLE 5. Body weights (kg) of immature and yearling Giant Canada Geese before spring migration.

Age and sex	Dates of capture			
	8-16 February	23-26 February	1-16 March	23 March-4 April
Immature				
Males	4.08 ± 0.07 ^a n = 11	3.98 ± 0.06 n = 26	4.52 (4.08-4.87) n = 3	4.76 (4.54-4.98) n = 2
Females	3.50 ± 0.08 n = 14	3.34 ± 0.07 n = 21	4.08 ± 0.22 n = 7	4.31 (3.98-4.63) n = 2
Yearlings				
Males	4.16 (3.87-4.66) n = 3	3.61 (3.61-3.61) n = 2	4.80 (4.15-5.18) n = 3	4.54 (4.26-5.08) n = 3
Females	3.71 (3.35-4.02) n = 4	3.34 ± 0.14 n = 9	4.08 ± 0.12 n = 5	4.52 n = 1

^a Mean ± SE (range when n < 5).

content of geese collected in mid-February was 17% and 14% for females and males, respectively. Lipid levels of female and male geese collected just prior to migration were 29% and 22%, respectively. This increase in lipids accounted for 61% of the weight gained by females and 47% of the weight gained by males. Protein contributed 10% (females) and 13% (males) of the increased weight, and water 21% and 35% of the weight gained by females and males, respectively. Lipid levels were consistently more variable than protein levels among geese within collection groups, especially in females (Table 6).

Increases in lipids did not occur uniformly throughout the study period despite significant correlations with weight gain (females, $r = 0.92$, $P < 0.01$; males, $r = 0.77$, $P < 0.01$). In females, 75% of a 230-g increase from 12-16 February to 4-7 March (Table 6) was water, 22% was protein, and the average weight of lipids actually decreased 10%. Males gained 734 g in the same period, 66% of which was water, 19% protein, and only 8% lipid. In contrast, of the increase in average body weight between 4-7 March and 4-6 April, lipids contributed 75% of 1,091 g gained by females and 89% of 691 g gained by males. Water contributed 9% and protein 8% of weight gained by females. For males, comparable values were 2% and 7%, respectively. Increases in protein and water were highly correlated for all adult geese ($r = 0.95$, $P < 0.01$). The unexplained percentage of weight gains in the above analyses was due to an increase in feather weight during spring.

Skeletal muscle masses.—Weights of dissected right leg muscles of collected geese (Table 7) differed significantly among collection periods ($F = 6.48$, $P < 0.01$) and between sexes ($F = 49.38$, $P < 0.01$). The increase in weight of leg muscles was highly correlated with body weight gain for both females ($r = 0.83$, $P < 0.01$) and males ($r = 0.96$, $P < 0.01$) and differed significantly between sexes ($F = 5.62$, $P < 0.01$), males gaining more than females.

Right breast muscle weights (Table 7) were also significantly different among collection periods ($F = 6.45$, $P < 0.025$) and between sexes ($F = 35.27$, $P < 0.01$). Similarly, breast muscle weight was correlated with body weight (females, $r = 0.90$, $P < 0.01$; males, $r = 0.85$, $P < 0.01$). Also, gains in breast muscle weight tended to differ between sexes ($F = 2.07$, $P < 0.1$). Water content was highly correlated with protein in breast muscle ($r = 0.96$, $P < 0.01$). Breast lipids were correlated with total body lipid content ($r = 0.84$, $P < 0.01$). The change in weight of protein of breast muscles, however, did not parallel increases in total body protein during

TABLE 6. Body weight (less gut contents) and composition (g) of adult Giant Canada Geese collected in spring.

Sex and component	Collection period			
	12-16 February	4-7 March	14-16 March	4-6 April
Female	<i>n</i> = 5	<i>n</i> = 4	<i>n</i> = 6	<i>n</i> = 4
Body weight ^a	3,712 (179)	3,942 (74)	4,381 (129)	5,033 (88)
Lipid	3,252-4,117 ^b	3,845-4,160	4,009-4,901	4,725-5,243
Protein ^c	642 (88)	619 (110)	951 (50)	1,442 (56)
Water	774 (22)	824 (21)	858 (27)	911 (13)
	1,969 (71)	2,141 (90)	2,216 (63)	2,242 (39)
				2,164-2,342
Male	<i>n</i> = 3	<i>n</i> = 5	<i>n</i> = 2	<i>n</i> = 2
Body weight ^a	4,149 (144)	4,883 (107)	5,200; 5,134-5,266	5,574; 5,424-5,725
Lipid	580 (90)	639 (98)	881; 797-964	1,253; 1,133-1,372
Protein ^c	966 (52)	1,106 (18)	1,112; 1,067-1,156	1,156; 1,079-1,233
Water	2,269 (18)	2,757 (35)	2,824; 2,702-2,947	2,774; 2,577-2,972

^a Differences between body weight and the sum of components are due to weight of feathers and organs removed prior to analysis.

^b Mean (SE when *n* > 2) range.

^c Protein = lipid-free residue (see Raveling 1979a).

TABLE 7. Weight and composition (g) of skeletal muscles of adult Giant Canada Geese collected in spring.

Sex and muscle	Collection period			
	12-16 February	4-7 March	14-16 March	4-6 April
Female	<i>n</i> = 5	<i>n</i> = 4	<i>n</i> = 6	<i>n</i> = 4
½ Leg ^a	179 (8) 151-199 ^b	183 (7) 168-198	199 (8) 172-230	220 (8) 205-243
½ Breast ^a	361 (17) 303-396	371 (15) 351-415	385 (11) 355-426	450 (14) 408-474
Composition				
Lipid	16 (2) 10-20	17 (2) 13-21	21 (2) 13-28	31 (3) 26-37
Protein ^c	96 (3) 86-105	98 (5) 90-111	100 (3) 92-113	116 (3) 106-122
Water	248 (12) 207-273	256 (11) 240-287	264 (8) 244-292	303 (13) 268-328
Male	<i>n</i> = 3	<i>n</i> = 5	<i>n</i> = 2	<i>n</i> = 2
½ Leg ^a	202 (7) 195-215	245 (7) 222-259	266; 261-271	298; 271-325
½ Breast ^a	428 (22) 406-472	474 (11) 442-509	460; 430-489	536; 510-562
Composition				
Lipid	20 (3) 17-25	18 (2) 15-25	15; 14-17	29; 28-29
Protein ^c	115 (5) 108-125	127 (3) 120-138	120; 113-127	139; 132-146
Water	294 (14) 279-321	329 (7) 304-347	324; 301-348	369; 350-387

^a Right side only.^b Mean (SE when *n* > 2) range.^c Protein = lipid-free residue (see Raveling 1979a).

spring. Between the 12-16 February collection and the 4-7 March collection, only 8% (4 g in females) and 17% (24 g in males) of the gain in total lipid-free residue could be attributed to an increase in the protein of breast muscles (right breast content \times 2, Table 7). Dramatic enlargement of digestive organs in this period (McLandress and Raveling, unpublished) may indicate a site of much of the protein uptake. From 4-7 March to 4-6 April, the protein increase in breast muscle was 41% (36 g, females) and 48% (24 g, male) of the total gain in protein.

Reproductive energetics.—Ryder (1970) suggested that the clutch size of Ross' Geese evolved in relation to reserves that females accumulate before arriving on the breeding grounds. Incubating geese also depend on stored reserves and are near starvation weight by the time their eggs hatch (Raveling and Lumsden 1977, Ankney and MacInnes 1978, Raveling 1979a). Therefore, according to these ideas, body reserves of reproductive adult geese prior to nesting should contain the components required for migration, egg laying, and incubation.

Reserves needed to meet the energy demand of migratory flight are a relatively small proportion of the total reserves accumulated in spring (Raveling and Lumsden 1977). This would be especially true for this population because of the relatively short distance between winter and summer ranges (855 km); additionally, migration was frequently interrupted (Wege 1979), and birds were observed feeding enroute. Major departures from Rochester occurred on 2 and 6 April, and major arrivals on the nesting grounds occurred on 8-9 April.

King (1973) calculated that 373 kcal of energy were required to form a 163-g egg of *B. c. canadensis*. The mean weight of fresh eggs of Giant Canada Geese of this study population is 168 g (calculated from Cooper 1978: 56). Formation of an average clutch of 5.6 eggs (Cooper 1978) would thus require 2,153 kcal (373 kcal \times 168/163 g \times 5.6 eggs). Eggs of domestic geese contain 12.0% lipid, 12.2% protein, and 12.4% shell material (Romanoff and Romanoff 1949). With these values, an average clutch of Giant Canada Goose eggs would thus contain 113 g lipid, 115 g protein, 117 g shell material, and 1,723 kcal energy (estimating lipids at 9.5 kcal/g and

protein at 5.65 kcal/g; Ricklefs 1974). Catabolism of an additional 48 g body lipids would be required to supply the necessary 430 kcal of energy (2,153 kcal - 1,723 kcal) for egg formation (at 9.0 kcal/g; Ricklefs 1974). Lipid reserves accumulated in spring (800 g) would be more than adequate to contribute to egg lipids, the energetic cost of egg formation, and maintenance until the beginning of incubation. The 137 g of lipid-free residue accumulated in spring by female Giant Canada Geese, however, is insufficient to supply the total 232 g of mineral (117 g) plus protein (115 g) requirements of an average clutch of eggs. The weights of bones removed during dissection did not differ among collections. The change in weight of ovaries, due largely to yolk deposition, was 23 g (12-16 February: $n = 5$, $\bar{x} = 5$ g, range = 2-7 g; 4-6 April: $n = 4$, $\bar{x} = 28$ g, range = 13-43 g) and accounted for less than 5 g of additional stored protein and minerals (yolk contains 18.0% protein, 1.6% mineral; Romanoff and Romanoff 1949). Similarly, protein and mineral requirements of clutches of Cackling Geese could not be supplied by stored reserves (Raveling 1979a). Therefore, supplements must be obtained from body components maintained through winter and/or from feeding on the nesting grounds. The disparity between the amount of protein plus minerals required for egg laying and the amount of lipid-free residue gained by females in spring may be partly explained by undetected mineral accumulation. Roots eaten by geese before the initial February collection may have provided partial or sufficient mineral reserves for egg laying. Minerals so obtained would have been part of the initial lipid-free residue content of February collected birds and would thus have been excluded from calculated increases of lipid-free residue.

In a study of Cackling Geese, Raveling et al. (1978) concluded that medullary bone is extensively deposited during the last half of rapid ova development (6-7 days) and is depleted after laying. The absorption of calcium and phosphorus from the digestive tract of domestic hens is greatly increased immediately before egg laying (Taylor and Moore 1954). Thus, minerals required for egg production may be obtained on the nesting grounds during or slightly before egg formation. In either case, the calculated gain in weight of lipid-free residue of female geese prior to spring migration would be mostly protein. This gain in body protein (137 g) was only slightly greater than the protein requirements of an average clutch of eggs (115 g), which supports the contention that pre-breeding accumulated protein reserves are probably a major factor limiting clutch size (Jones and Ward 1976, Raveling 1979a).

Alternatively, some of the protein required for egg formation might be obtained on the nesting grounds. Wypkema and Ankney (1979) reported that total dry weights of breast, leg, and gizzard muscles of Lesser Snow Geese increased at spring staging areas just before departure for the breeding grounds but that wet weight of subcutaneous, mesenteric, and abdominal fat did not change. Based on these indices, they concluded that fat was being maintained while protein was stored. Our data indicate, however, that the later stage of hyperphagia (14-16 March to 4-6 April in this study) is a period of extensive lipid storage. Although the weight of breast and leg muscles increased, 38% (females) and 42% (male) of the gain of the "dry" components was lipid (Table 7). Furthermore, the increase in water content of the breast muscles alone (females: 39 g \times 2; males: 45 g \times 2) exceeded any increase in total body water content (females gained 26 g and males actually lost 50 g of water, Table 6). Therefore, some of the protein increase (with associated increase in moisture) of the skeletal muscles may have been transferred from other body tissues.

Shifts among protein "pools" have been suggested in other studies of geese (Hanson 1962a, Raveling 1979a). Some of the late gain in muscle protein was probably protein transferred from digestive organs, which decreased in size in the last weeks of hyperphagia (McLandress and Raveling, unpublished). Thus, the change in indices used by Wypkema and Ankney (1979) exaggerates total body protein storage because it does not account for lipids in the muscles or transfer of protein from other tissues.

The mean weight of fat (1,442 g) in a female Giant Canada Goose of maximum spring weight less the amount of fat required for egg production (161 g) would leave 1,281 g to provide energy for migration and maintenance during the period from arrival on the breeding grounds to the end of incubation. This amount is essentially equal to the average 1,253 g of fat in adult males collected just prior to spring migration. Maximum spring weights recorded at the time of arrival on Arctic nesting areas of colonial nesting Lesser Snow Geese (Ankney and MacInnes 1978) and Ross' Geese (Ryder 1967) and the more dispersed nesting Cackling Geese (Raveling 1979a) reveal that males weigh slightly less than females. In this study, the two male Giant Canada Geese collected immediately before spring migration (4–6 April) weighed 5.4 and 5.7 kg and averaged 541 g heavier than the four females collected. An additional two males collected 15 April on the nesting grounds weighed 5.4 and 5.6 kg. In all goose species, comparisons of body measurements and autumn weights show that males are larger than females (Bellrose 1976). Thus, Giant Canada Goose males appear to accumulate more spring reserves, relative to reserves of the female, than do males of other species and races of Canada Geese. The hypothesis that reserves acquired by the male are limited to the maximum weight that can be carried during periods of migration (Ryder 1975) seems unlikely, as females are structurally smaller than males of Arctic-nesting geese yet weigh more at arrival on nesting grounds. Perhaps the maximum weight attained by males initially evolved in relation to the reserves necessary for maintenance and territorial defense before food became available on the nesting grounds. Ryder (1975) suggested that territories were important for supplemental food that may be required by male Ross' Geese to enable their continual attendance near the nest during incubation. The high energy reserve of male Giant Canada Geese could have evolved in response to greater predation pressures and/or lack of food in the marsh nesting territories and enabled more devoted attention to nest defense without leaving to feed. Alternatively, it may have evolved by providing the capability for additional defense necessary to maximize food acquisition by the female for renesting in the event of nest failure. Large Canada Geese, unlike Arctic-nesting geese, often renest when nest destruction occurs during or before incubation (see Bellrose 1976 for review). These additional reserves could be attained by large Canada Goose males consuming more food and/or using less energy during the spring fattening period than would males of the smaller Arctic-nesting geese. Measurements of body composition changes of males of both large and small species of geese during nesting would clarify the adaptive significance of different energy use strategies in relation to food availability and predation.

Male Giant Canada Geese gained proportionately more protein (lipid-free residue) than females during spring. The increase in protein during the first stage of hyperphagia (up to 7 March) was 2.8 times greater in males than in females. The portion of this protein gain, attributed to hypertrophy of breast and leg muscles (assuming similar composition to breast muscles, Table 7), was 9.1 times greater in males than females. Weight gains in breast and leg muscles were more comparable between

sexes for the remainder of the period of hyperphagia. Hanson (1962a) concluded that hypertrophy of breast muscles in *B. c. interior* during spring was the result, at least in part, of muscle use in migration. At least part (if not all) of the increase in muscles of Giant Canada Geese occurred before migration stresses, however. Accumulations of muscle protein are no doubt more important as sources of egg protein in females, and territorial defense in males, than for the stresses of the relatively short migration of Giant Canada Geese. The earlier improvement in body condition of ganders may be associated with the defense of feeding sites necessary for successful prereproductive preparation of the female.

CONCLUSIONS

Protein appears to be more limited than lipids with respect to requirements of reproduction. Additionally, protein may be necessary for increasing the efficiency of converting carbohydrate from corn or other food sources (e.g. bulrush) to fat during hyperphagia in spring. In our study, new-growth grass was the food source that provided high levels of protein. We believe that the availability of new grass is essential in allowing Canada Geese to obtain the body reserves necessary for early migration and nesting before food is generally available on the breeding grounds.

Age and social factors may influence the amount of food consumed by geese in spring. Behavior and lower body weights of young geese and unmated adults indicate that they obtained less food than did mated adults before spring migration. Thus, access to grass in spring, age, and social history are among the proximate factors affecting accumulation of body reserves and attainment of reproductive condition by Canada Geese.

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