

WINTER WEIGHT DYNAMICS, GRAIN CONSUMPTION AND REPRODUCTIVE POTENTIAL IN CANADA GEESE

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ABSTRACT.—Hanson (1962) suggested that late winter weight loss of Canada geese (*Branta canadensis*) is a normal situation in which geese enter a refractory period that later facilitates rapid weight gain during vernal migration. To examine this hypothesis, winter weight dynamics, grain intake, and indices of physical and reproductive condition were compared for 13 caged Canada Geese maintained on three feeding schedules: (1) ration unlimited January through 11 May; (2) ration restricted during January/February but unlimited thereafter; and (3) ration restricted throughout the trial but quantity increased progressively from March through May.

Geese fed freely did not reduce their intake during late winter, but maintained food consumption and gained weight from January through April. The data suggest that late winter weight loss in these geese is not necessitated by endogenous factors, but instead reflects food availability and ambient conditions. Weight loss in February or March does not elicit rapid weight gain in April. Reduced intake in January and February ultimately had little effect on breast and organ weights, carcass lipid and protein, and indices of reproductive potential. However, the reproductive potential of two females kept on restricted intake through May possibly was affected, as indicated by lighter ovary weights, with fewer and smaller follicles.

Nearly 90% of the Canada Geese (*Branta canadensis*) in the Mississippi Valley population spend the winter at Crab Orchard, Union County, and Horseshoe Lake refuges, Illinois (Kennedy and Arthur 1974). Geese begin to arrive in mid-September when refuge crops and waste grain supply abundant food (Bell and Klimstra 1970, Sauer 1983). By mid-March, most geese are migrating to the breeding grounds in northern Ontario, where they arrive in early May. Hanson (1962) found that birds of all sex-age classes, especially females, were considerably heavier in spring on the breeding grounds than in mid-November to mid-January at Horseshoe Lake. That geese should be heaviest, with extensive fat reserves, upon arrival at the breeding grounds is consistent with observations for other species (Ryder 1970, Harvey 1971).

Elder (1946), however, noted that weights of all sex-age classes of Canada Geese at Horseshoe Lake Refuge decreased significantly during January to March. Hanson (1962:27, 42) suggested that winter weight losses might be normal and that geese might be in a "refractory period," which later facilitates rapid gain of weight and fat during or before spring migration. Raveling (1968) agreed and cited Williams' (1965) data regarding penned geese that

had fed freely as support of this contention. However, Williams' data for an unspecified number of captive geese showed that both sexes gained weight from October to March. Thus, the data do not unequivocally support the idea that winter weight loss or lack of gain is normal.

If control of late winter body weight in Canada Geese is principally endogenous, then voluntary weight loss should occur despite unlimited access to food. However, if reduced winter weights are caused by limited food supplies coupled with low ambient temperatures, then access to an adequate diet should prevent weight loss. Birds should be heaviest in April or May in preparation for reproduction (Hanson 1962, Raveling 1979a, b).

In this study, we evaluated Hanson's (1962) hypothesis of endogenous weight regulation before spring migration. Nine Canada Geese were fed grain freely throughout winter and spring to determine whether body weight and consumption conformed to the pattern suggested by Hanson. Ration levels for an additional five geese were reduced during January/February to simulate weight losses reported by Elder (1946). To investigate weight recovery, ration levels were then increased and maintained unlimited for three of the five geese,

TABLE 1. Chemical properties of basal ration fed to Canada Geese during January–May 1982.^a

Ration period	Dry matter (%)	Gross energy (kcal/g)	Crude protein (%)
January	91.6	4.51	9.7
February	87.0	4.60	6.7
March	88.4	4.48	9.5
April	90.2	4.47	9.1
May	90.2	4.47	9.1

^a Relative composition of the ration averaged 87% cracked and whole corn, 5.6% sunflower seed, 4.5% wheat, 2.9% milo, and grit.

and increased progressively from March through 11 May for the other two.

METHODS AND MATERIALS

Adult Canada Geese (*B. c. interior*) were captured during October and November, 1981. On 1 December, they were weighed, and sexed and aged using plumage and cloacal characteristics (Hanson 1965). Birds were placed into elevated, individual wire pens (1.8 m × 1.5 m × 1 m) constructed of 2.54-cm welded wire covered with 1.5-cm hardware cloth. Each goose was provided water and commercial hen feed (hereafter called basal ration) consisting of cracked and whole corn (*Zea mays*; 87%), sunflower seeds (*Helianthus annuus*; 5.6%), wheat (*Triticum aestivum*; 4.5%), milo (*Sorghum vulgare*; 2.9%), and grit. The ration was supplemented with vitamins A, D, niacin, and riboflavin. Basal ration was replaced at three-to-five-day intervals throughout the trial. Birds were weighed once every 7 to 10 days. The study was initiated on 1 January and terminated on 11 May 1982.

Of the 14 geese originally in this study, five died owing to injuries in January and two were removed owing to severe, progressive weight loss (>30%). Of the remaining seven, two (1 female, 1 male) were on unlimited intake and five (3 females, and 2 males) were fed a restricted intake. To supplement sample sizes, we randomly selected six geese (4 females, 2 males) from birds used in feeding trials run concurrently under identical conditions (Joyner, unpubl.). Live weights of the six geese were averaged over each month and monthly means compared statistically (*t*-tests) with weights of geese fed freely. Because there were no significant differences ($P > 0.05$), the six geese were incorporated into the sample of geese fed freely. The six birds were fed over the four-month trial the same basal ration given to the unlimited group, except during 4–9 and 17–22 January, 24 February–2 March, 20–26 April, and 1–11 May when the six geese were fed monotypic rations of whole corn, wheat or milo.

Monotypic rations did not affect rates of feeding.

The five geese on restricted intake were supplied basal ration at the rate of 106 g/day (dry weight) during January and 74 g/day in February. February feeding levels were reduced to simulate reported midwinter weight losses (Elder 1946, Hanson 1962). On 1 March, rations were unrestricted for three of the five geese (two males, one female). Because it is questionable whether migrating geese encounter food freely during spring, rations for the other two females were increased weekly over the trial, and averaged 111 g/day in March and 125 g/day in April and May. Duplicate subsamples of each month's food were ground through a Wiley mill with 1-mm screen openings, and analyzed for composition. Percent moisture was determined by vacuum-drying subsamples to a constant weight at 100°C (Horwitz 1980). Gross energy was measured using a Parr adiabatic oxygen bomb calorimeter. Nitrogen content was determined by modified Kjeldahl technique involving sample digestion with a mixture of phosphoric and sulfuric acids (5:100), distillation, and titration with standardized hydrochloric acid using a mixed indicator (Table 1).

All geese were killed on 11 May 1982, and the carcasses were weighed and frozen for subsequent analysis. Each carcass was thawed, plucked, weighed to the nearest gram, and selected organs (liver, empty gizzard, heart, left testis or ovary), left breast muscles (pectoralis, supracoracoideus, coracobrachialis), and visceral fat (excluding fat attached to mesenteries and organs) removed and weighed (g wet weight). The digestive tract was removed and emptied. Additional measurements (mm) taken were length and width of testis or ovary, diameter of ovarian follicles ≥ 2 mm, width of oviduct 25 mm anterior to the cloacal/oviduct junction, and length of culmen, tarsus, and middle toe. Age and sex were verified through dissection.

Carcasses were sectioned using hand shears, and each carcass including internal organs and visceral fat was homogenized using an electric food chopper. Duplicate 100-g samples were taken from the homogenate and frozen, pending analysis. Moisture content of carcasses was determined by drying duplicate samples to a constant weight at 100°C (Horwitz 1980:125). Carcass nitrogen content was determined as described above, and crude protein calculated as nitrogen content multiplied by 6.25. Carcass lipid content (ether extract) was determined according to Horwitz (1980:376). Statistical analyses (*t*-test, univariate analysis of variance

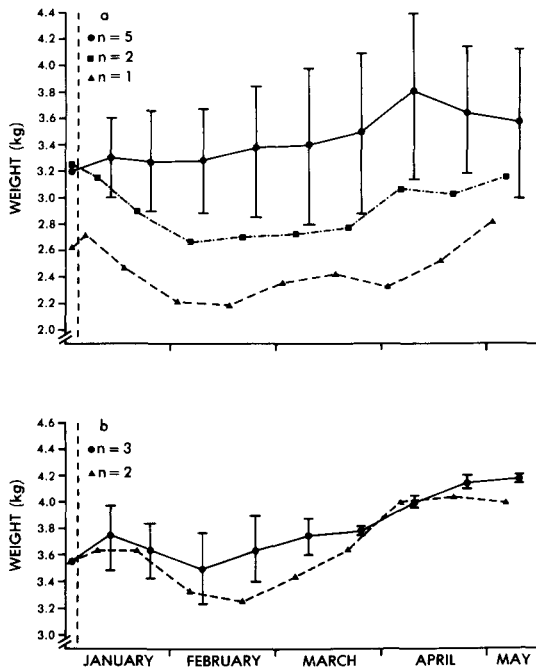


FIGURE 1. Mean live weights of eight adult female (a) and five male (b) Canada Geese, 1 January through 11 May 1982. (●) Geese fed unlimited basal ration. (▲) Rations averaged 106 g/day (dry weight) in January, 74 g/day in February, and unlimited thereafter. (■) Rations averaged 106 g/day in January, 74 g/day in February, 111 g/day in March, and 125 g/day thereafter. Symbols within the vertical dash line represent respective live weights on 31 December 1981. Vertical lines represent ± 1 SD.

with Student-Newman-Keuls test) follow Sokal and Rohlf (1969).

RESULTS

WEIGHTS

The five females fed freely gained weight steadily from January through March (Fig. 1a). Peak weights in mid-April were heavier (12%) than in January or February ($F_{4,29} = 2.92$, $P \leq 0.05$). These females subsequently lost some weight in late April and May. Females on restricted intake were lightest in February and gradually regained weight after rations were increased (Fig. 1a). The two kept on restricted intake regained 78% of the weight lost during January and February, while the single female fed freely after 1 March regained all weight lost and exceeded pretrial (31 December) weight by 3%. Peak weights of females on unlimited feed exceeded pretrial weight by 15%. Although the females retained on restricted intake were lighter in February, March, and April than the five females fed freely ($P \leq 0.05$, t -tests), live and carcass weights (weight of carcass less gut contents and plumage) did not differ significantly in May ($t = 1.17$, $t = 1.22$, respectively,

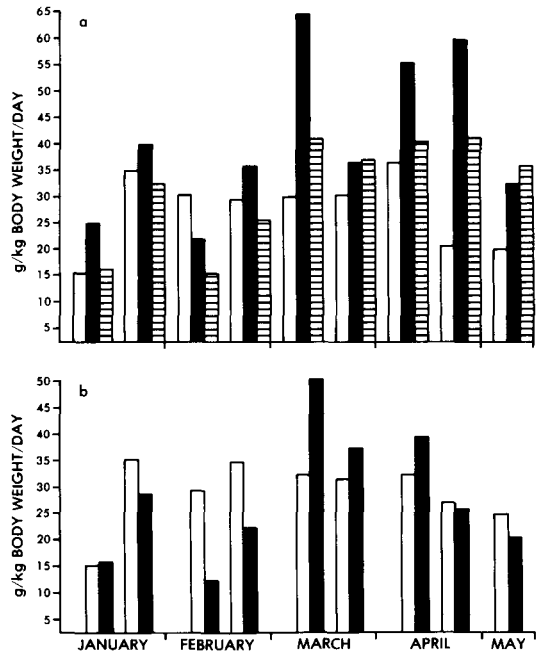


FIGURE 2. Average daily consumption for eight adult female (a) and five male (b) Canada Geese, 1 January through 11 May 1982. Open bars = five females and three males fed freely. Solid = one female and two males fed 106 g/day (dry weight) during January, 74 g/day during February, and unlimited thereafter. Hatched = two females fed 106 and 74 g/day during January and February, respectively, 111 g/day in March, and 125 g/day in April and May.

6 df, $P > 0.05$). Carcasses of females fed freely were, however, 13% heavier than those of females kept on restricted intake.

Males on both ration levels gained some weight in early January (Fig. 1b). Both groups lost weight in February, but losses were significant only for males on restricted intake ($F_{4,30} = 6.63$, $P \leq 0.05$). Males fed freely attained peak weight in May and were heavier ($F_{4,55} = 23.48$, $P \leq 0.05$) than at any other time during the trial. Males initially on restricted intake attained peak weight in April. Carcass weights differed ($t = 4.32$, 3 df, $P \leq 0.05$) between the two groups with males on restricted intake weighing less.

GRAIN CONSUMPTION

Intake (g dry matter, DM) varied by sex for geese fed freely, with males generally consuming more basal ration than females (119 vs. 107 g/day). This was expected because males averaged 20% heavier and thus required more energy (Williams and Kendeigh 1982). However, relative to body weight (Fig. 2), consumption was comparable between the sexes. We could see that consumption by geese fed freely frequently oscillated such that peak pe-

TABLE 2. Body weights (g) and composition (g wet weight) of adult Canada Geese fed restricted intake (R) or unlimited (U) ration levels, January through 11 May 1982.^a

Ration	n	Sex	Mean carcass wt. ^b	Water		Crude protein		Lipid	
				%	Wt.	%	Wt.	%	Wt.
R ^c	2	F	2,875	56	1,600	18	518	24	676
R ^c	1	F	2,600	57	1,475	18	475	22	575
U	5	F	3,300	52	1,725	17	575	25	850
R	2	M	3,700	49	1,825	16	586	31	1,150
U	3	M	3,925	51	2,000	18	700	27	1,050

^a Refer to Table 1, Figure 1, for composition of ration and ration levels.

^b Weight of carcass less gut contents and plumage; all weights rounded to nearest 25 g.

^c Ration levels for the first two geese were increased progressively during March and April; the single female received unlimited ration after 1 March.

riods of intake (one to two days) were usually preceded and succeeded by periods (two to three days) of lower intake. This normally had little effect on live weights. However, when consumption was excessively low (e.g., 35–50 g DM/day) over a three-day feeding period, individuals usually lost 2–3% of their weight. Geese subsequently maximized intake during the succeeding three days (160–180 g DM/day) and recovered previous weight losses. Only in late April and May did intake drop (\bar{x} = 95 g DM/day) and remain low, precipitating progressive weight loss. All 24 caged geese ate less in May, regardless of the grain supplied (basal ration or monotypic diet used in feeding trials).

Intake averaged over semimonthly intervals did not vary significantly from mid-January through April for geese fed freely (Fig. 2), but was greater during that period than during 1–15 January or May (females, $F_{8,34} = 4.15$; males, $F_{8,18} = 2.76$; $P \leq 0.05$). We found no evidence of a prolonged reduction in intake followed by “hyperphagia” during February, March or April.

Consumption by geese on restricted intake followed a predictable pattern (Fig. 2). When food was limited, most or all of each day's ration was consumed, especially in February when rations were restricted to 74 g/day. Geese previously on restricted intake ate twice as much in March when ration was unlimited (Fig. 2, solid bars), and thereafter generally consumed more than was eaten by geese fed freely. The females kept on restricted intake continued to consume most or all of each day's ration, except in May when as much as 20% of each day's ration remained in feed trays (Fig. 2a, hatched bars).

CARCASSES

Wet weights of breast muscles (left side), visceral fat, and selected internal organs (excluding the liver) were consistently lighter in geese on restricted intake compared to birds of the

same sex continually fed freely. Except for the gizzard (females, $t = 3.31$, 6 df, $P \leq 0.05$) and pectoral muscles (males, $t = 3.68$, 3 df, $P \leq 0.05$), differences were not significant. Livers of geese on restricted intake were not significantly heavier. Ovaries of the three females on restricted intake weighed less (1.4 vs. 2.5 g, $t = 0.73$, 6 df, $P > 0.05$), contained smaller developing follicles (6.3 vs. 7.5 mm, $t = 1.30$, 27 df, $P > 0.05$) and had fewer follicles (4.0 vs. 5.3/bird, $t = 3.33$, 6 df, $P \leq 0.05$) than females fed freely.

Birds on restricted and unrestricted diets did not differ in percent carcass water, crude protein, or lipid (Table 2). However, on an absolute wet weight basis the freely-fed females contained 10% more protein and 20% more lipid than those on restricted intake. Live weights of these two groups were equal in late December (Fig. 1a). Freely-fed males supported 16% more protein than those on restricted intake, but 9% less lipid.

DISCUSSION

Recent studies suggest that winter weight loss is a common phenomenon among temperate-wintering birds (Peterson and Ellarson 1979, Dugan et al. 1981, McLandress and Raveling 1981b, Sauer 1983). Reinecke et al. (1982) found that adult female Black Ducks (*Anas rubripes*) wintering in Maine lost 15% of their fall weight during December and January; such losses were attributed to an endogenous rhythm that reflected shifts in expected benefits of an energy reserve compared to the costs of carrying additional weight. McLandress and Raveling (1981b:68) stated that Canada Geese will lose weight in winter regardless of food availability. This was not the case, however, when caged Canada Geese were supplied unlimited grain from January through early May (see Fig. 1). In fact, weight generally increased during this period. Freely-fed birds attained peak weight in mid-April. Wild Canada Geese are also heaviest in April or May just before breed-

ing, often reflecting a rather abrupt increase over winter weights (Hanson 1962, Raveling 1979a, b, McLandress and Raveling 1981b, Thomas and Prevett 1982).

The freely-fed males gained 8 g/day during March and April, whereas the females averaged 6 g/day. A similar pattern showing comparable weight gains between male and female *B. c. maxima* was reported by McLandress and Raveling (1981b). Female *maxima* wintering in Minnesota gained 36 g/day, whereas males averaged 26 g/day. These geese gained weight rapidly soon after melting snow exposed grass at feeding sites. Presumably, they had lost weight because food was scarce before March. Caged *interior* gained weight to a lesser degree, presumably reflecting the unlimited food supply available to the geese throughout winter, and the slightly smaller stature of this race.

Weight changes in geese on restricted intake were predictable. As ration was withheld, maintenance costs exceeded energy intake and geese lost weight. When ration was increased, geese ate more. Weight gain in males was rapid, averaging 15 g/day during March and April. By early April, live weights of the two males were comparable to weights of males on unrestricted food. After feeding freely, the female gained 7 g/day during March and April. She eventually regained all weight lost during January and February, and by May, exceeded pre-trial weight by 3%. However, the females kept on restricted intake failed to recoup weight losses even though consumption (g/kg body weight/day) during March and April equalled or exceeded that of geese on unrestricted food (Fig. 2). They gained a little weight in March as ration levels were increased, and rapidly grew heavier in April (mean for March and April = 8 g/day), the same time when females who had fed freely attained their maximum weight. Intake, however, did not increase significantly in April for either group. Whether or not the females would ultimately have attained pre-laying live weights comparable to those of the females fed freely is unknown.

We found some evidence for differential capacity in late winter weight recovery between males and females following deprivation. Males recovered weight rapidly and completely by April; females were less successful. This contrasted with McLandress and Raveling's (1981b) findings for free-flying *B. c. maxima*. By progressively increasing basal ration supplied to two of the three females initially on restricted intake, we may have consequently influenced their ability to recover weight rapidly. However, by comparing (Joyner, unpubl.)

existence energy requirements based on Ken-deigh's (1970) equation for nonpasserines to daily energy retention for these two geese (kcal/day, apparent metabolizable energy estimated from feeding trials run concurrently with this study), we found that daily energy retention during March and April exceeded requirements. Thus, the two birds shifted from a negative energy balance in February to a positive one in March and April. Consumption by the single female initially on restricted intake but later fed freely generally exceeded that of other geese during March and April (Fig. 2), yet her rate of weight gain for that interval was only 7 g/day. Sauer (1983) also found differential capacity for weight recovery in Canada Geese on Horseshoe Lake Refuge, Illinois, during a period of severe weather in February, 1982. When a previously inaccessible grain supply was exploited, live weights of females increased 11% over 14 days, males increased 18%. The permanent pair bond and dominance hierarchy in Canada Geese may serve as a mechanism to counter this disparity since before and during migration, light-weight paired females gain enough time to forage so as to replenish lipid and protein reserves depleted during winter (Raveling 1970, Palmer 1976, McLandress and Raveling 1981a, b). Yearlings, being less likely to nest (Bellrose 1976), would not be under the same selection pressure, and weight gains necessary for maintenance and migration would suffice.

Except during 1–15 January (Fig. 2), intake by geese who fed freely remained relatively constant throughout winter, which counters Hanson's (1962) suggestion of voluntary reduction in intake in late winter followed by hyperphagia. The five females who fed freely consumed the most ($P > 0.05$) in early April, however, presumably reflecting their need for lipid and protein deposition before reproduction (Hanson 1962, Harvey 1971, Ankney and Bisset 1976).

Our data suggest that mid-winter weight loss in *B. c. interior* is largely influenced by food availability and ambient conditions, whereas the rapid weight gains in April or May are induced by endogenous and exogenous factors acting synergistically. Variability in winter weights between years or within the season can easily be attributed to differential rates of metabolic, digestive, and foraging efficiency, as they relate to food availability and prevailing ambient conditions. The fact that the live weights of geese wintering in southern Illinois during 1982–1983, a mild winter, gradually increased from October through February (e.g., adult females, $n = 397$, \bar{x} weights = 3.53, 3.59, 3.52,

3.68, and 3.65 kg, respectively; Estel 1983) supports this conclusion. In addition, weight depression in February or March does not appear mandatory to induce rapid weight gains in April.

Lastly, carcass composition (Table 2) suggests that a reduced food supply in January and February did not affect reproductive potential in May. Lipid requirements for a clutch of five eggs represent at least 140 g, or 1865 kcal (McLandress and Raveling 1981b:74-75). Carcass lipid levels for the geese on restricted intake averaged 625 g in May, which should have been sufficient for a 5-egg clutch. Carcass protein also appeared adequate, and was comparable to levels recorded for *B. C. maxima* in early April (McLandress and Raveling 1981b). However, the results are not unequivocal given the collective potential effect of lighter ovary wet weights, with fewer and smaller follicles of females on restricted intake. Since rapid yolk synthesis begins in the ovaries of large birds 7 to 10 days before ovulation (King 1973: 89), and geese were not allowed to undergo normal nesting activity, the true reproductive potential of females on restricted intake is uncertain.

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