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THE UNIVERSITY OF ALBERTA

THE IMPACT OF DIET DURING THE NESTING CYCLE ON THE PRODUCTIVITY OF CANADA GEESE

BY

ANDREW MURPHY

A THESIS
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE IMPACT OF DIET DURING THE NESTING CYCLE ON THE PRODUCTIVITY OF CANADA GEESE submitted by Andrew Murphy in partial fulfillment of the requirements for the degree of Master of Science.

Supervisor

Mark V. H. Wilson

Cynthia Paszkowski

Date: April 19, 1988

Abstract

Experimental manipulations of food quality and quantity were used to assess the impact of diet on reproductive variables of Canada geese (*Branta canadensis*) nesting in captivity. The study also investigated the use of body reserves and amount of food ingested by wild female Canada geese during incubation, as well as the relationship between body weight and condition in these latter birds.

Both quality and quantity (availability) of the pre-laying diet influenced the reproductive output of captive Canada geese. Captive female geese required high levels of digestible energy in the diet before and during laying in order to realize full reproductive potential. Egg size and number, and nest attentiveness were reduced when geese relied on herbage diets that contained less digestible energy than the control diet. Despite an abundance of high quality food, enriched to meet their requirements, captive female geese lost an average of more than 700 g over the laying period, suggesting that they were relying, in part at least, on body reserves. A physiological constraint on the amount of food consumed may force females to rely on body reserves at this time.

During incubation, female *B. c. moffitti* nesting near Brooks, Alberta derived 87 % of their energy requirement from body reserves, more than that used by any other subspecies of Canada goose studied to date. The use of exogenous food was negligible during early incubation but quite variable during the final week of incubation.

Body weight was significantly correlated with the condition (fat content) of wild females at the beginning of incubation, but not at the end of that period. Correcting for body size by using morphometric measurements did not improve significantly the relationship between body weight and condition.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

I. Introduction

Many birds rely on endogenous nutrient stores (body reserves) to meet some or all the nutrient demands of reproduction (King 1973). This tactic is widespread among waterfowl (eg. Harris 1970, Drobney 1980, Krapu 1981, Tome 1984), and is particularly prominent in geese (eg. Hanson 1962, Ryder 1970, Harvey 1971, Ankney 1977, Raveling and Lumsden, 1977). Investigations of this phenomenon in various subspecies of Canada geese (*Branta canadensis*) have revealed significant differences in the timing and magnitude of both the accumulation and the use of body reserves (Bromley 1984, Mainguy and Thomas 1985).

Hanson (1962) and Raveling and Lumsden (1977) suggested that nesting interior Canada geese (*B. c. interior*) relied almost exclusively on body reserves, acquired prior to their arrival on the breeding grounds, to meet nutrient demands during the pre-laying, laying, and incubation periods. Bromley (1984), on the other hand, determined that dusky Canada goose females (*B. c. occidentalis*) augmented fat reserves considerably after they arrived on the breeding grounds. Further, during the laying and incubation periods, both female cackling (*B. c. minima;* Raveling 1979) and female dusky Canada geese (*B. c. occidentalis;* Bromley 1984) relied as much on food available on the breeding grounds as on body reserves acquired before arrival.

The use of body reserves during reproduction has frequently been interpreted as an indication of nutritional stress (eg. Hanson 1962, Harris 1970, Korschgen 1977), but King and Murphy (1985) questioned this interpretation. They emphasized that catabolism of nutrient reserves is sometimes a routine tactic employed in the presence of abundant food resources. They also stressed that birds (and other endotherms) normally enjoy a "buffer" between nutrient availability and nutrient demand, and that they can employ compensatory behavioral adjustments to alleviate nutrient scarcity.

Mainguy and Thomas (1985) found that digestive organs of female giant Canada geese (*B. c. maxima*) collected early in the laying period were larger in a year of low pre-breeding fat reserves. These investigators attributed the increased size of digestive organs to increased feeding intensity, that is, increased volume of food consumed per unit time, the stimulus promoting increase in gut biomass (Fenna and Boag 1974). This suggests that giant Canada goose females have the ability to compensate for annual variation in pre-breeding body reserves as late as the early laying period. Since female dusky Canada geese augment their body reserves on the breeding grounds before and during the early part of the laying period (Bromley 1984), these females may also be able to compensate for reduced body reserves as late as the early laying period.

Canada geese may also possess the ability to compensate for low body reserves during the incubation period. Sherry et al. (1980) demonstrated that incubating Burmese red junglefowl (*Gallus gallus spadiceus*) responded to the depletion of their body reserves by increasing their food intake. The observations of Aldrich and Raveling (1983) suggest that incubating Canada geese can also employ this kind of compensatory tactic. These investigators found that rate of weight loss and incubation attentiveness were related to body weight (an index of body reserves) throughout the incubation period. Aldrich and Raveling (1983) assumed that increased food intake during longer and more frequent incubation recesses enabled females with lower body weights to reduce their rate of weight loss.

Since nutrient allocation for self-maintenance usually takes precedence over demands for reproduction among iteroparous animals (King and Murphy 1985), it is reasonable to expect nesting Canada geese to respond to a nutritional challenge by reducing their nutrient expenditure for reproduction. Clutch size has been linked with levels of food intake (eg. Bengston 1971, Nisbet 1973, Rohwer 1984, Winkler, 1985) and body reserves (Jones and Ward 1976, Ankney and MacInnes 1978, Jarvinenn and Vaisanen 1984). Ricklefs (1974) stated that egg size was maintained at the expense of clutch size, but Nisbet (1973), Houston et al. (1983), and Murphy (1986) have demonstrated reductions in egg size that they attributed to poor nutritional status.

Bromley (1984) estimated the cost of incubation of dusky Canada geese at only 1.25 basal metabolic rate (BMR). Incubation is not costly in terms of energy expenditure, but it involves extremely high nest attentiveness (Cooper 1978, Aldrich and Raveling 1983, Bromley 1984), which severely restricts the time female geese can devote to foraging. Reducing nest attentiveness in order to increase foraging time exposes the clutch to increased risk of predation (Ryder 1970, Harvey 1971, Inglis 1977) and reduces egg hatchability (Harvey 1971, MacInnes et al. 1974). Thus, incubating geese must balance their reliance on food intake against the effects of reduced nest attentiveness (required for obtaining food) on egg predation rates and egg hatchability.

In this study, I investigated the pattern of body reserve and food use by western Canada geese (*B. c. moffitti*) nesting in captivity. Several investigators (Raveling 1979, Aldrich 1983, Bromley 1984) have estimated the nutrient intake of nesting geese indirectly, by subtracting the nutrients supplied by body reserves from the estimated total nutrient demand. I measured food consumption of nesting geese directly and converted this to nutrient intake based on digestibility of the diet. I also investigated the ability of the geese to compensate for reductions in their food source (both quantity and quality) during nesting. This required experimental manipulations of the food supply. I exposed captive Canada geese to a nutritional challenge (decreased food quality and/or availability), and recorded their food intake, weight dynamics, egg production and nest attentiveness. These experiments are reviewed in Chapter II.

To compare the captive situation with that of wild Canada geese in surrounding habitat, I estimated the quantities of body reserves and food used by wild females during incubation (Chapter III). A sample of females was collected at the beginning and at the end of incubation. The difference in energy reserves (the energy available from the catabolism of fat and protein reserves) in the two samples was used to estimate the energy that this population of female Canada geese derived from body reserves over the course of incubation. The weights of ingesta in the guts of these females and the number of recesses taken per day were used to estimate the energy that they derived from food intake during the early part of the incubation period and in the final week of incubation.

I also used the females collected from the wild to evaluate the relationship between body weight and body condition, and attempted to improve the relationship between body weight and condition by incorporating morphometric measurements (Chapter IV).

Chapter V integrates the results of these studies with those of other studies and discusses the implications of the results for goose biology.

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II. THE IMPACT OF DIET MANIPULATION DURING THE NESTING CYCLE ON FOOD INTAKE, WEIGHT DYNAMICS, EGG PRODUCTION, AND NEST ATTENTIVENESS IN CANADA GEESE

Introduction

The use of body reserves during nesting has been documented in all subspecies of Canada geese studied to date (*B. c. interior* - Hanson 1962, Raveling and Lumsden 1977; *B. c. minima* - Raveling 1979; *B. c. occidentalis* - Bromley 1984; *B. c. maxima* - Mainguy and Thomas 1985) and in other goose species as well (eg. Ankney and MacInnes 1978, Ankney 1984). Several investigators (Hanson 1962, Ryder 1970, Ankney 1977, Raveling and Lumsden 1977) have taken this use of body reserves to indicate low food availability on the nesting grounds. However, King and Murphy (1985) emphasized that the use of nutrient reserves (for reproduction and for other activities) is often a normal event in the annual cycle and that it can evolve in response to either unusually high nutrient demands or to competing demands from other activities as well as low food availability.

Among geese, incubation for example, is an activity incompatible with normal feeding activity. High nest attentiveness is needed to ensure successful reproduction (Ryder 1970, Harvey 1971, Inglis 1977). This prevents incubating females from meeting their nutrient requirements from food ingestion and forces them to rely on body reserves. The use of body reserves during incubation is mediated by a gradual reduction in the set point for body weight (the weight that individuals endeavor to maintain). This produces anorexia among incubating females (Sherry et al. 1980). The extent to which incubating females rely on body reserves during incubation varies considerably among species and subspecies (see Thompson and Raveling 1987 for review), and even varies within a subspecies depending on the level of body reserves with which females begin incubation (Aldrich and Raveling 1983). Incubating females are reported to invest all their available reserves in incubation, relying on food intake to meet any shortfall in these reserves for nutrient requirements (Aldrich 1983).

While the use of food and body reserves during incubation seems to be independent of food abundance (Mainguy and Thomas 1985), it is not clear how food abundance and food quality influence the reliance upon food versus body reserves during laying. Investigators working in the central Canadian arctic (Hanson 1962, Ryder 1970, Ankney 1977, Raveling and Lumsden 1977) concluded that low food availability prevented geese from exploiting food resources profitably during laying. However, Mainguy and Thomas (1985) reported that giant Canada goose (*B. c. maxima*) females relied on body reserves during laying despite an abundant food supply. Hence, low food abundance is not sufficient to explain the use of body reserves in all situations.

Several investigators have reported that female geese devote most of their time to feeding during laying (Inglis 1977, Fox and Madsen 1981, Aldrich 1983, and others). This suggests that laying females may be maximizing their foraging effort, but it does not indicate necessarily that they are suffering from a shortage of food per se. Bromley (1984) suggested that food quality might be more important than food quantity during laying. Since increasing selectivity reduces the rate of food acquisition (Owen 1972), the relatively large amount of time spent feeding may be a reflection of very selective foraging for a preferred food in short supply rather than a response to general food scarcity.

This study imposed a variety of diet treatments on a flock of captive breeding western Canada geese (*B. c. moffitti*) in order to establish how food abundance (or availability) and food quality (energy and protein content) influenced the use of food and body reserves by nesting geese. Body reserves were also manipulated in some situations in order to evaluate the extent to which geese could adjust food intake to compensate for reduced body reserves. Egg production and nest attentiveness were monitored in order to assess the impact of diet and/or body reserve manipulations on productivity.

Methods

This study was conducted at the Brooks Wildlife Centre (BWC) near Brooks, Alberta. The geese were reared (by Alberta Fish and Wildlife) from wild eggs collected in the Brooks area. Nearly all of the geese were between 7 and 13 y old when the experiment began and had nested at the BWC previously. They were individually identifiable by leg bands and neck collars. I collected data on their food intake, weight dynamics, and reproductive output during the nesting seasons of 1984, 1985, and 1986 (Table II-1).

1984

The geese were given access to 25 outdoor breeding pens on March 20. Pairs were allowed to select their own pens, and were confined to breeding pens when they were seen occupying the same pen on 2 consecutive days (a procedure leading to successful reproduction at the BWC in previous years). By March 27, 22 pairs had been confined to breeding pens. One additional pair was confined on April 1.

Each pen measured 9.2 x 9.2 m, and contained a 2.2 x 2.3 m concrete pond, a nesting structure (an automobile tire containing flax straw), and a gravity flow self feeder containing a pelleted waterfowl breeder ration. The sides of the individual breeding pens were made of 1.2-m chain link fencing. Green vegetation was not evident in breeder pens when geese were confined, but it became evident in unoccupied pens shortly after the experiment began. In occupied pens it was not evident until after females had begun incubation, having been consumed by the geese as it grew until this time.

Feeders were constructed of galvanized sheet metal and held 10 kg of pelleted food (commercially prepared waterfowl breeder ration). The ration was enriched in amino acids important for egg production (methionine, lysine, and tryptophan). Geese obtained food through a 5-cm hole that was protected by a 15 x 20 cm metal rainguard. The position of this hole (approximately 4 cm above the level of the pellets) prevented spillage of food. Feeders were

Table II-1: Reproductive output[1] and food consumption of captive Canada geese in response to pre-laying and laying diet: objectives and predictions.

Year	Objectives	Diets[2,3]	Predictions
1984	Record food consumption during nesting and maximum reproductive output	Control	High rate of food consumption until females begin incubation, very high reproductive output
	Record food consumption and reproductive output for second nesting attempts	Control	Greater food consumption throughout egg formation and reduced reproductive output
1985	Record food consumption during nesting and maximum reproductive output	Control	High rate of food consumption until females begin incubation, very high reproductive output
	Test effects of reduced food availability	LA	Decreased food consumption, decreased reproductive output
	Test effects of reduced food availability and reduced digestible energy	Alfalfa	Decreased food consumption if availability limits food use/increased food consumption if energy demand regulates consumption
	Test effects of reduced body reserves	RC	Increased food consumption, decreased reproductive output
	Test effects of reduced body reserves followed by a low protein diet	RK	Increased food consumption, decreased reproductive output (especially egg hatchability)
1986	Test ability of geese to increase body reserves and then nest on a diet of new growth grass	Wheat-grass	Significant increase in body weights, reduced food intake during laying (relative to pre-laying period), decreased reproductive output

[1] Refers to all of the following: proportion of pairs nesting, clutch size, egg size, nest attentiveness and incubation behavior.

[2] Refer to text for a description of the diet treatments.

[3] Digestible energy and crude protein contents provided in Table II-2.

mounted 40 cm off the ground. This prevented small mammals from removing food. A steel screen roof and chain link fence, enveloping the breeding pen facility, exoluded large birds. A few house sparrows (*Passer domesticus*) were occasionally seen within the facility, but they did not seem to be attracted to the pellets provided for the geese, which may have been too large for them to ingest. The amount of food consumed was recorded when feeders were filled at weekly intervals using a 2-l juice can graduated in tenths that held an average of 1040 g (± 8.5 g N = 10) of the ration. Feeders, mounted adjacent to alleys, could be filled without entering the pens, thus reducing disturbance to the geese.

Each pen was searched for freshly laid eggs each day from April 1 until the female occupying the pen had completed her clutch. These searches were always conducted in the early afternoon. Eggs were labeled with a waterproof felt marker and weighed to the nearest gram (300 g spring scale graduated in 2-g intervals) as they were found. Clutch sizes were recorded and considered complete when 3 d elapsed without addition of new eggs. First clutches were removed upon completion to encourage production of a second clutch (Table II-1). Females were weighed on a Pesola 5-kg spring scale (100-g increments) when their first clutches were removed.

Females that produced a second clutch and their mates were weighed 3 d after the final egg of their second clutch was found. I attempted to separate females that were incubating second clutches from their mates with 2.6 x 2.6 m snowfence enclosures in order to record the food consumption of females and males separately. This procedure was abandoned in subsequent ~~years~~ because of high rates of nest desertion (apparently the result of disturbance associated with construction of enclosures).

1985

All adult Canada geese used in the 1985 experiment were weighed on February 20, 1985. Geese that weighed less than 5 kg were weighed on the 5-kg Pesola scale used in 1984. Individuals that weighed more than 5 kg were weighed on a Gold Brand 12-kg platform scale to the nearest 25 g.

Geese were confined to individual breeding pens in the same manner as in previous years. Three diets were used initially in 1985 (a control and two treatments - Table II-1). The control was the same diet that the geese had received in previous years except that two feeders (rather than one) were installed in each pen to prevent any potential competition at the food source between members of each pair. These feeders, containing the commercially-prepared waterfowl breeder pellets, were mounted 40 cm off the ground. One (low availability = LA) treatment diet tested the effects of reduced food availability of the same commercially-prepared breeder pellets (Table II-1). Pellets were provided in feeders identical to those used for the control group. However, feeders were mounted 72 cm off the ground, making it much more difficult for geese to remove pellets from the feeders and thereby reducing the number of pellets that geese were able to remove per unit time. The second treatment consisted of a diet of dehydrated alfalfa (*Medicago sativa*) pellets provided in feeders also mounted 72 cm off the ground. This treatment (Table II-1) tested the effect of low food availability plus low digestible energy content (approximately half that of the commercially-prepared breeder pellets) in the food (Table II-2).

Diets were assigned by stratified randomization (on the basis of 1984 clutch initiation dates). Oyster shell was provided to ensure that all females had access to an abundant supply of calcium regardless of their diet. The two feeders, mounted 1 m apart in each pen, ensured that members of each pair did not need to compete for feeding opportunities. Feeders were filled in the same manner as in 1984. Initial diet treatments (Table II-1) commenced on March 31, 1985.

The two treatment diets caused large reductions in weight of some pairs. These weight losses forced reassignment of these pairs to higher energy diets (Table II-1). Four pairs initially assigned to the LA diet and nine pairs initially assigned to the alfalfa diet were reassigned randomly to either the commercially-prepared

Table II-2: The digestible energy and crude protein content of foods provided for nesting Canada geese.

			Composition (dry matter basis)	
Food	Diet Treatment(s) & Yr(s).	% moisture	Dig. Energy (kcal/kg)	Crude Protein (%)
Breeder Pellets[1]	Control 84,85 LA & RC 85	10.5	3039	16.0
Alfalfa Pellets[2]	Alfalfa 85	9.4	1521	18.9
Flaked Corn[3]	RK* 85	11.5	3450	9.8
Crested Wheatgr.[4]	Grazed grass 86	65.7	1711	24.9 to 14.0

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[1] Based on manufacturer's guaranteed analysis.

[2] Calculated from data presented in Marriott and Forbes (1970).

[3] Based on Morrison (1958).

[4] % Moisture from Morrison (1958); Digestible Energy calculated from total energy (Coupland 1973) and retention rate (Owen 1980); Crude protein determined by sampling (see Table II-7).

breeder pellets or flaked corn (*Zea mays*) provided in feeders 40 cm off the ground. These diets are hereafter referred to as reassigned control (RC) and reassigned corn (RK) diets (Table II-1). The RC diet allowed me to assess the ability of the geese to compensate for reduced body reserves when they had ready access to a high quality food source. The RK diet assessed effects of a high energy but low protein diet (Table II-2) on the reproductive cycle of Canada geese that had suffered losses in body reserves (Table II-1).

All geese in these experiments were weighed on March 30 and at weekly intervals thereafter using a Gold Brand 12 kg platform scale. Pairs were not weighed while the female of the pair was laying. In 1985, each female was allowed to incubate its first clutch. Both members of a pair were weighed 3 d after the last egg of the clutch was found and at weekly intervals thereafter during incubation.

Three Sankyo super-eight movie cameras, equipped with interval timers, recorded incubation behavior of selected females. Cameras (enclosed in adapted ammunition boxes) were installed 2.3 m off the ground in alleys between pens. Cameras exposed one frame every 60 seconds from dawn to dusk.

1986

Only 16 of the 24 pairs that produced clutches in 1985 were retained in 1986. Geese were maintained on the same commercially-prepared waterfowl breeder ration used in previous years (Table II-1). One of the paired male geese was found dead on February 17. Mean weights of both males and females, taken on March 1, 1986, were greater than corresponding weights taken on February 20, 1985, indicating that the geese were in as good or better condition than the year before.

My objective in this year was to assess the ability of the geese to acquire pre-laying reserves after March 27 and subsequently to nest on a diet of new-growth grass (Table II-1). In order to evaluate the ability of the geese to acquire pre-laying reserves, I had to reduce the reserves acquired overwinter. From March 1 until March 15, I restricted food consumption of these geese (N = 31) to approximately 152 g of breeder pellets/individual/d. Food was scattered across the pen in midafternoon to assure that each individual had an opportunity to feed. This amount represented 65% of the ad libitum (ad lib.) intake of the same food by post nesting pairs in the previous year. This food restriction did not reduce the mean weight of females. Mean body weights of females actually increased (from 4342 to 4511 g) despite this food restriction. This forced me to impose an even more stringent food restriction on the geese in order to reduce the body reserves of females (Table II-1). As weights and condition indices of females were rather variable, I segregated pairs into three groups of five pairs each, on the basis of the female's body condition. I used body weight divided by tarsus length as the condition index. The previously paired female (mate died in February) was in good condition and was included as a sixth female in the group of five pairs that had high condition indices.

Groups were taken from the common winter pen and placed in three adjoining breeder pens on the morning of March 16. The high, medium, and low condition index groups received 300, 800, and 1250 g (27, 80, and 125 g/bird), respectively, of the pelleted ration each day from March 16 until March 27 (Table II-1). In midafternoon, food was scattered widely across the entire pen to encourage uniform distribution of food among individuals.

On March 27 all geese in this experiment were weighed and released into a large (150 x 124 m) outdoor grazing pen. The diet restrictions had reduced the mean weights of females and males by 314 ± 229 g and 194 ± 250 g, respectively, relative to their March 30, 1985 weights.

The grazing pen contained a roughly circular pond approximately 45 m in diameter. Oyster shell and calcareous grit were scattered around the perimeter of the pond, but no pelleted food was provided until all females had completed incubation.

Females, and their mates, were weighed at weekly intervals from March 27 until each female began laying. Geese were captured for weighing by herding them into a snow fence enclosure in one corner of the grazing pen. A 20-m wing fence facilitated their capture. Females were also weighed at weekly intervals from Day 3 until Day 24 of incubation. Males were weighed only on Day 3 and Day 24 of incubation as they were difficult to capture without a great deal of disturbance. Incubating females were easier to capture, normally remaining on their nests until approached within a few meters. This greatly facilitated their capture (by long-handled dip net) and minimized the disturbance of neighboring pairs; incubating females on adjacent nests nearly always remained on their nests during capture, weighing, and release of their incubating neighbor.

The grazing pen was thoroughly searched daily for freshly laid eggs. Eggs were marked and weighed as they were found.

On alternate days, the 10 freshest feces, encountered during the daily search for freshly laid eggs, were sealed individually in plastic bags and frozen (within 1 h of collection). They were later oven dried (56° C) to constant weight. The weights of these feces were used in conjunction with defecation rates to calculate the dry weight of grass ingested by geese.

Vegetation samples were collected at approximately 1-wk intervals. Each vegetation sample consisted of eight subsamples. The grazing pen was divided into eight areas of uniform size, and one subsample was collected from each of these areas. A 20 x 20 cm wire grid was randomly positioned within 10 m of the center of each area and all of the green, above ground vegetation was clipped from within the grid. Vegetation samples were sealed in plastic bags and frozen within 1 h of collection. They were later oven dried (56° C) to constant weight, passed through a Wiley mill (60 mesh screen) and analyzed (moisture, protein, fiber and lignin concentrations) by the Alberta Provincial Feed Testing Laboratory.

A 20X spotting scope was used to observe the geese from a 4-m observation tower in the pen. Scan sampling (Altman 1974) was used to record the behavior of the geese. Four pairs were selected for observation during each observation bout. Preference was given to pairs that appeared to be ready to lay (male vigorously defending a nesting territory and female's abdomen bulging) or were already laying. The behavior of each member of each pair was recorded at 4-min intervals for 1 h. These observations were made on alternate days, and were performed during the early morning, midday, and late afternoon time periods according to a rotating schedule. The categories used to describe the activity of the geese were feeding, alert, loafing, attending nest, and other. The other category included all forms of locomotion, interaction with other individuals, preening, drinking, etc.

Once the majority of paired females had begun incubation (April 29), another series of observations was initiated. They were performed in the same manner as above except that only incubating females that were on incubation recesses were observed.

Another set of observations was used to estimate the defecation rates of females that appeared to be preparing to lay or were already laying. Active females (those that were neither loafing nor attending the nest) were watched continuously and each defecation was recorded. A new focal bird was selected each time it became impossible to reliably record each defecation of a given focal bird. These observations were not performed according to a fixed schedule, but an effort was made to make them at various times throughout the day. Defecation rates were calculated from these observations by the hourly-block method (Bédard and Gauthier 1986). These defecation rates were used in conjunction with feces weights to estimate the dry weight of vegetation ingested by females during the pre-laying and laying periods.

Observations were always performed either before or at least 2 h after birds were disturbed. No observations were made until 10 min after the observer entered the tower. The behavior of the geese seemed to return to normal within 1-2 min after the observer was out of site in the tower.

As in 1985, super-eight movie cameras were used to record the incubation behavior. The cameras, in ammunition boxes, were placed directly on the ground 3-5 m from nests of incubating females. Cameras were positioned in the evening and were moved every fifth day. Each roll of film recorded the attentiveness of a particular female for four diurnal periods. Cameras did not seem to have any influence on the behavior of incubating females. Many females remained on their nests while cameras were installed. Females that left their nests during the installation of cameras returned to their nests without hesitation as soon as the camera was installed and I had retreated from the area.

Subdivisions of the Nesting Cycle

In 1984 and 1985, I recorded the weekly food intake of confined pairs on the same day of each week throughout the experiment. Likewise, all pairs were weighed on the same day of each week until the female of the pair produced her first egg. Since pairs began and completed laying on different days of the week, the food intakes and pre-laying weights that I recorded were not precisely synchronized with each female's nesting cycle.

Feeders were always filled at 7 d intervals. Follicle maturation (the period of accelerated yolk deposition) takes approximately 13 d in Canada geese (Bromley 1984). Hence it spanned roughly two of the food consumption intervals. The food consumption interval that coincided most nearly with the first half of the follicle maturation period is referred to as the early yolk deposition (EYD) period. The food consumption interval that coincided most nearly with the second half of the follicle maturation period is referred to as the rapid yolk deposition (RYD) period. The laying (LYG) period and the first to fourth weeks of incubation refer to successive 7-d intervals after the RYD period.

Since pairs were not weighed during laying, the term laying period, used with regard to body weight, was of variable length and did not correspond entirely with the laying period as it was applied to food consumption data (1984 and 1985) or feeding behavior (1986). It included, on average, about 3 d before the appearance of the first egg, the entire period of laying plus the first 3 d of incubation (in all about 13 d). I use the term pre-laying period to refer to the 7-d period that preceded the last weighing before clutch initiation.

There were four weekly food consumption periods in the incubation period, but only three weekly incubation weight losses. This difference reflected the need to delay weighing of the geese until 3 d after the appearance of the last egg (to ensure that the clutch was complete) and from the fact that the geese were last weighed on Day 24 of incubation rather than the hatch date (Day 27).

Statistical Methods

All statistical procedures were performed using the SPSSx statistical package. A probability level of 0.05 was used to evaluate statistical tests. Means are reported ± standard deviations in the text and in tables, and ± standard errors in figures.

Results

1984

During the first nesting attempt, pairs consumed an average of 2.5 kg/wk of commercially-prepared breeder pellets over the EYD and RYD periods (Fig. II-1). Food consumption fell to 2.3 kg/wk during the laying (LYG) period, and then decreased sharply in the week that females began incubation (females were only allowed to incubate for 3 d before first clutches were removed). This pronounced decrease reflected the onset of incubation anorexia in females, a widespread phenomenon in birds (Sherry et al. 1980), and well documented in Canada geese (eg. Cooper 1978, Aldrich 1983). If one assumes the gander consumed about half of the food during the EYD period, and sustained this rate throughout, then, during period 0, the goose must have consumed virtually no food at all. Consumption rebounded the week after clutches were removed to pre-incubation levels, increasing gradually in subsequent weeks (Fig. II-1).

As predicted (Table II-1), food consumption rates were significantly greater during the EYD and RYD periods of second nesting attempts than during first nesting attempts (Table II-3). There is no reason to believe that these increases were the result

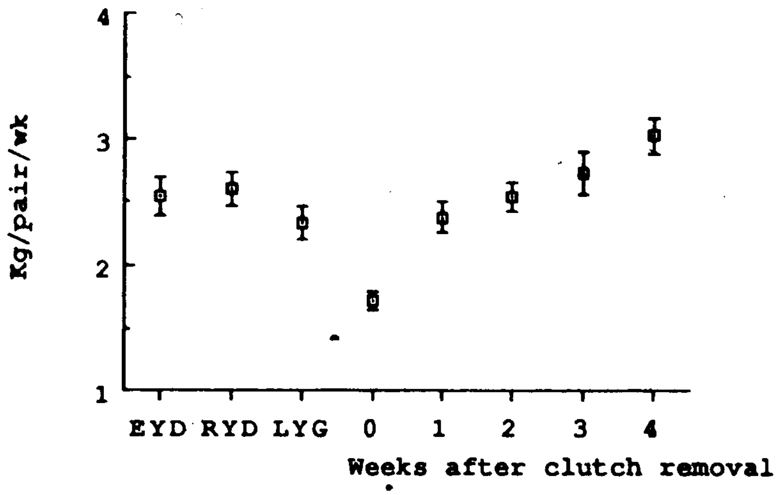

Fig. II-1: Food intake (mean ± SE) by pairs of Canada geese during early (EYD) and rapid (RYD) yolk deposition, laying (LYG), beginning of incubation (0), and weeks after clutch removal (1,2,3,4) in 1984. The first four points include data from all first nesting attempts (N = 21). The last four points include only pairs that did not lay a second clutch (N = 13).

Table II-3: Consumption (mean ± SD in kg/wk) of commercial pellets by pairs of Canada geese during first and second nesting attempts in 1984.

Week	# pairs[1]	First attempt	Second attempt	Difference	paired t	p[2]
Early yolk deposition	3	2.03 ± 0.23	2.60 ± 0.10	0.57 ± 0.25	3.90	0.030
Rapid yolk deposition	8	2.44 ± 0.48	3.05 ± 0.57	0.61 ± 0.61	2.86	0.012
Laying	8	2.23 ± 0.67	2.18 ± 0.57	0.05 ± 0.90	-0.16	0.879
Onset of incubation	7	1.86 ± 0.62	1.41 ± 0.32	0.44 ± 0.51	2.29	0.031

[1] Five of these pairs had already entered the "Early yolk deposition" period before food consumption was recorded. One female deserted her second clutch before the "Onset of incubation" period was complete.

[2] Greater food consumption during the first three periods was anticipated in response to body reserve depletion (during the previous nesting attempt). Reduced food consumption was expected during the fourth period because incubation behavior was maintained (second clutches were not removed, but first clutches were removed after 3 d of incubation), therefore one-tailed probabilities were used.

of increased ingestion rates of ganders, hence they probably reflected increased ingestion rates of geese (1.0 to 1.6 kg/wk during EYD and 1.4 to 2.1 kg/wk during RYD). Since females weighed an average of 187.5 g less (paired-t = 2.87, DF = 7; one-tailed P = 0.012) after completing their second clutch than after their first clutch, this increased food use probably reflects increased demand for exogenous nutrients to replenish (and/or compensate for) body reserves that were lost during their first nesting attempt.

Despite reduced female body weights (males were not weighed in 1984) and an ad lib. supply of high quality food, pairs did not use any more food during the laying period of second attempts than during first nesting attempts (Table II-3).

Pairs ate significantly less per week at the onset of incubation of their second clutch than they had at the onset of incubation of their first clutches (Table II-3). This reflects presumably the disruption of incubation anorexia in females when first clutches were removed after 3 d of incubation, an event that preceded the end of "0" week by approximately 3 d.

Food intake and weight dynamics-1985

Pre-laying and laying periods

Mean weights of both sexes (excluding one male hybrid and one male Canada goose that became ill), recorded on March 30, 1985, were 4.59 ± 0.42 kg (N = 26 females) and 4.97 ± 0.47 kg (N = 24 males). Four of nine pairs that were assigned initially to the LA diet failed to initiate a clutch on that treatment. During the first 2 wk of the experiment, food consumption by these pairs was significantly less than food consumption by pairs that did initiate nesting attempts on that diet (Table II-4). The difference was not significant during the third week because most of the pairs that nested had begun incubation by this time, an activity that produced anorexia in the female (Sherry et al. 1980). Nine of the 10 pairs assigned to the alfalfa diet also failed to initiate a clutch. These pairs were divided into two distinct groups on the basis of

Table II-4: Consumption of different diets (mean ± SD, or range if N < 4) by pairs of Canada geese that either failed to nest or did nest on initial diet treatments.

Diet & group	Week[1]	Failed to nest	No. pairs	Nested	No. pairs	P[2]
Low food avail-ability (LA) of commercial diet	1	0.9 ± 0.5	4	2.3 ± 0.6	5	0.003
	2	0.8 ± 0.5	4	1.8 ± 0.6	5	0.014
	3	1.0 ± 0.7	4	1.6 ± 0.4	5	0.088
Alfalfa-Group A (pairs eating < 250 g/wk)	1	0.1 ± 0.1	5	2.3 -	1	< 0.001
	2	0.1 ± 0.1	5	5.1 -	1	< 0.001
Alfalfa-Group B (pairs eating > 250 g/wk)	1	0.6 ± 0.4	4	2.3 -	1	< 0.001
	2	2.3 ± 0.3	4	5.1 -	1	< 0.001
	3	3.7 ± 0.6	4	5.2 -	1	0.008
	4	5.2 ± 1.3	4	6.9 -	1	0.040
	5	4.5 (3.4-5.5)	2	3.5 -	1	1.000

[1] The experiment began on April 1, 1985. Weeks 1, 2, and 3 corresponded with the early (EYD) and rapid (RYD) yolk deposition, and laying (LYG) periods for most of the females that nested on the LA diet. Weeks 3, 4, and 5 corresponded with the EYD, RYD, and LYG periods for the female that nested on the alfalfa diet.

[2] P values are one-tailed from pooled t-tests.

their food consumption. One group (A) consumed < 250 g/wk/pair in the first 2 wk of the experiment; the other group (B) consumed much > 250 g/wk/pair (Table II-4).

During the first 2 wk of the experiment, the single pair that did nest on the alfalfa diet ate significantly more than either of the two groups that failed to nest on that diet (Table II-4). This pair continued to eat more than other pairs (only pairs in group B remained on this diet) during the third and fourth weeks of the experiment, but by the fifth week, the pair that nested on this diet had begun laying and its food consumption fell markedly.

Considering only mean body weight, non-nesting female Canada geese on the LA treatment lost weight during the first and second weeks of the experiment. With one exception, these females gained weight in the third week (Table II-5).

Geese on the alfalfa diet that consumed < 250 g/wk/pair (group A) lost weight so rapidly that they had to be removed from that diet prior to the end of the third week (in most cases it was the condition of the male that necessitated the change).

Females on the alfalfa diet that consumed > 250 g/wk/pair (group B) lost nearly as much weight (mean = 281 g) during the first week of the experiment as females from group A (mean = 335 g). Unlike females in group A, females of group B increased their average weight in the second week of the experiment (Table II-5). However, the decline in the mean weight of Group B females resumed after the second week.

Approximately equal numbers of pairs nested on each of the control, LA, RC, and RK diets (Table II-6). These diets are hereafter referred to as the four main diet treatments. Since incubation induces anorexia among birds (Sherry et al. 1980), I analyzed food intake data from before initiation of incubation (when both members of the pair were presumably feeding) separately from that after incubation was initiated (when females were presumably feeding very little).

Both stage of the nesting cycle ($F = 4.19$ $DF = 2,35$; $P = 0.02$) and the diet treatment ($F = 3.14$ $DF = 3,19$; $P = 0.05$) had significant effects on food intake before incubation (Fig. II-2).

Table II-5: Changes in weight (g) of paired female and male Canada geese that failed to nest on their original diet treatments. Sample sizes appear in parenthesis beside means. Standard deviations (or range if N < 4) are in parenthesis below means.

Diet & group	Sex	Mar 30 to Apr 06	Apr 06 to Apr 13	Apr 13 to Apr 20	Apr 20 to Apr27	Apr 27 to May 04
LA	Female	-287 (4)	-213 (4)	+175 (3)		
		(± 97)	(± 159)	(-125,+375)		
	Male	-288 (4)	-150 (4)	+125 (3)		
		(± 237)	(± 158)	(-200,+525)		
Alfalfa Group A (pairs eating < 250 g/wk)	Female	-335 (5)	-230 (5)			
		(± 52)	(± 105)			
	Male	-531 (4)	-469 (4)			
		(± 97)	(± 185)			
Alfalfa Group B (pairs eating ≥ 250 g/wk)	Female	-281 (4)	+100 (4)	-88 (4)	-94 (4)	-75 (2)
		(± 97)	(± 159)	(± 85)	(± 88)	(-200,+50)
	Male	-417 (3)	-33 (3)	-100 (3)	-25 (3)	-125 (2)
		(-525,-300)	(-175,+50)	(-275,+75)	(-150,+125)	(-175,-75)

Table II-6: Proportion of pairs of Canada geese nesting on a variety of diet treatments.[1]

Treatment	Nested	Failed to nest	Total	Chi-square[2]	P
Control	7	0	7	0.7	0.380
Low food availability (LA)	5	4	9	14.5	< 0.001
Alfalfa	1	9	10	83.3	< 0.001
Reassigned to control (RC)	6	1	7	0.3	0.600
Reassigned to corn (RK)	5	1	6	0.5	0.488
Wheatgrass graze	14	2	16	0.3	0.589

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[1] Proportions are compared to the proportion of proven breeders that nested in 1984 (21 of 23).

[2] DF = 1

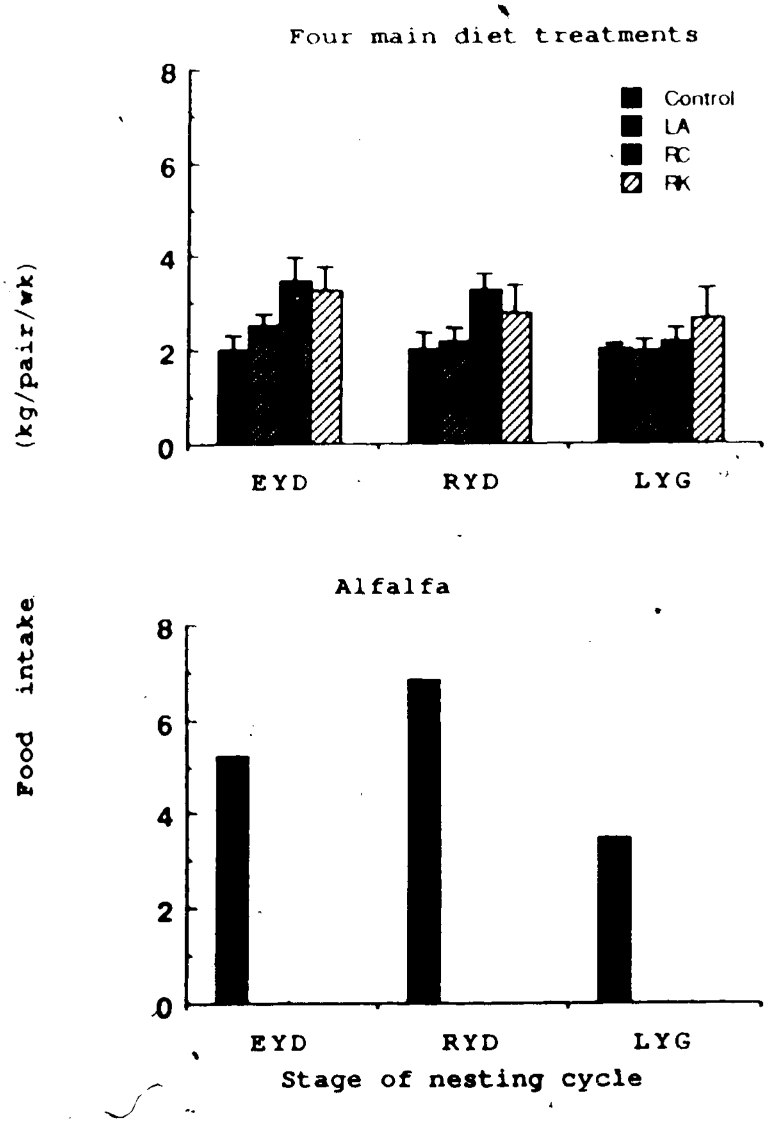

Fig. II-2: Food intake (mean ± SE) by Canada geese on the four main diet treatments, and on the alfalfa treatment (N = 1), during early (EYD) and rapid (RYD) yolk deposition, and laying (LYG).

Pairs reassigned to either the control or the corn diet (RC and RK, respectively) ate significantly more food than pairs nesting on the control diet (LSD range test), but only during the EYD and RYD periods (Fig. II-2). These observations from first nesting attempts resembled the pattern that was observed in second nesting attempts of 1984 (Table II-3). Birds with reduced body weights compensated for their reduced condition by eating more during the EYD and RYD periods, but they did not increase their food consumption significantly during the LYG period (Fig. II-2).

Increased food consumption allowed females of reassigned pairs to recover some of the weight they had lost on their original diets (Table II-5). The four main diet treatments (control, LA, RC, and RK) had a significant (F = 7.02 DF = 3,17; P = 0.003) effect on pre-laying weight gains of females. Specifically, females on RC and RK diets gained more weight (LSD range test) than females on control or LA diets (Fig. II-3), indicating that reassigned females were replenishing reserves concurrent with rapid yolk deposition.

Males of pairs that were reassigned tended to gain weight during the pre-laying period, while males on the control and the LA treatments just maintained weight (Fig. II-3). However, weight dynamics of reassigned males were variable (note standard error bars), rendering the apparent increase nonsignificant (P = 0.11).

There was no indication that the four main diet treatments (control, LA, RC, and RK) affected weight dynamics of females during laying (Fig. II-4).

There was a tendency for males reassigned to the control diet (RC) to gain weight during laying while males on other treatments tended to lose weight (Fig. II-4), but analysis of variance indicated that this difference was nonsignificant (P = 0.09).

Only one pair nested on the alfalfa diet. I used a series of t-tests to compare the food intake per week of this pair to the food intake per week of the control group. This pair ate more food than the control group (all P values < 0.001) during all stages of egg formation (including LYG period), but the difference was far more pronounced during the EYD and the RYD periods than during the LYG period (Fig. II-2). The alfalfa diet contained far less digestible

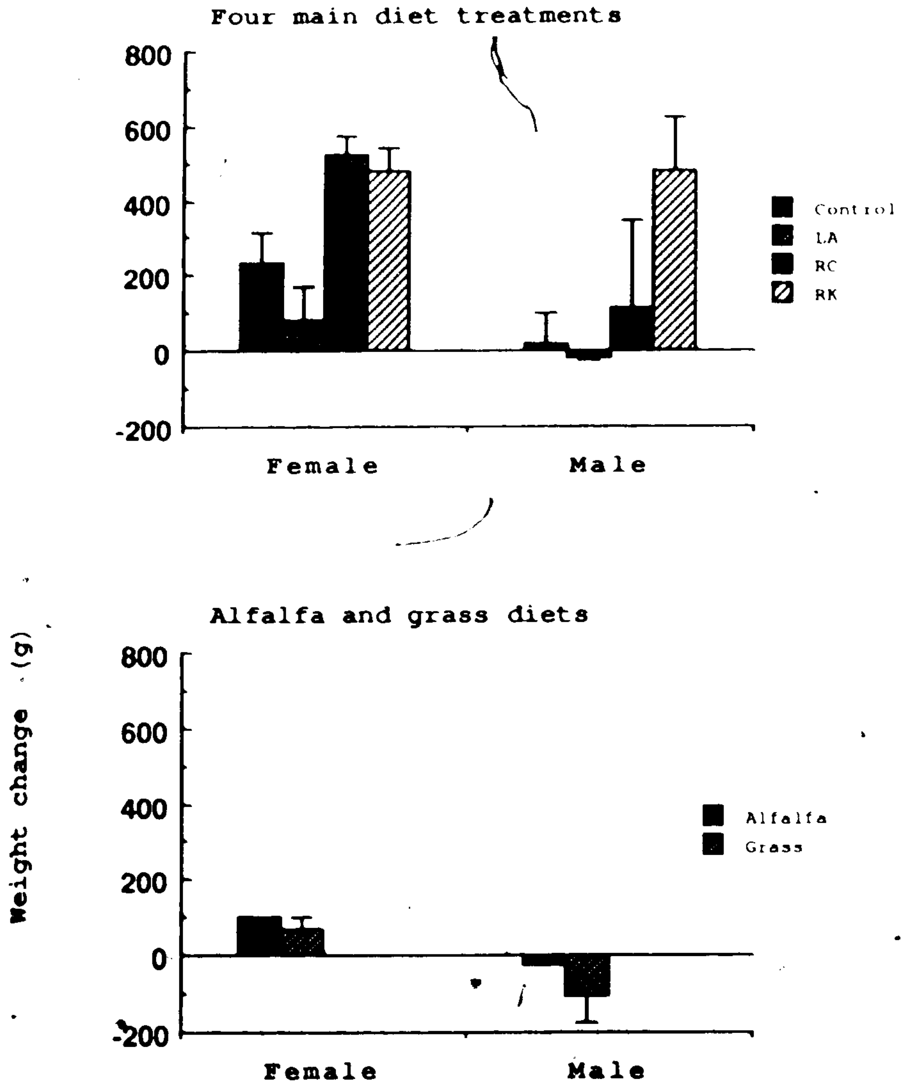

Fig. II-3: Weight changes (mean ± SE) of Canada geese nesting on the four main diet treatments and on alfalfa and grass diets during the week before clutch initiation occurred.

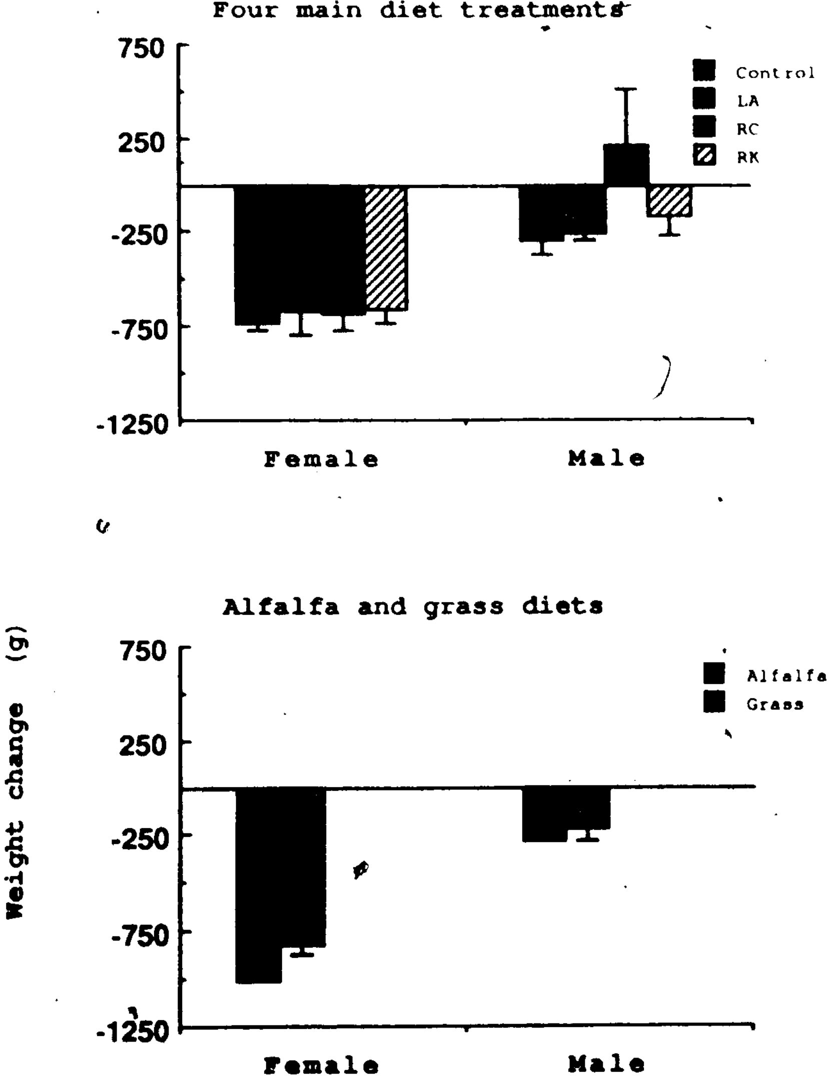

Fig. II-4: Weight changes (mean ± SE) recorded over the laying period in Canada geese nesting on the four main diet treatments, and on alfalfa and grass diets.

energy, but more protein than the control diet (Table II-2). The large differences in food consumption during both the EYD and RYD periods suggest that the pair was compensating for the lower energy content of the alfalfa diet. The female that nested on the alfalfa diet increased her body weight between the initiation of diet treatments and clutch initiation, and the male maintained his body weight during this period. This suggested that the pair was successfully compensating for the lower digestible energy content of the diet prior to clutch initiation by eating much larger volumes.

The dramatic decrease in food intake per week by this pair between periods RYD (6.9 kg/wk) ~~and LYG~~ (3.5 kg/wk) indicates that the onset of laying influenced their (one or both members of the pair) ability to compensate for reduced diet quality (by ingesting more food). The weight dynamics of the pair (Fig. II-4) suggest that it was mainly the female that was unable to continue to compensate successfully for the lower quality of the alfalfa diet. The female lost significantly more weight ($t = 7.11$ DF = 6, $P < 0.001$) than control females (despite producing fewer, and smaller eggs, Table II-7), but the male lost roughly as much weight as control males. This supports the evidence from renesting and reassigned pairs that the use of food by females is reduced during laying, but suggests that this male continued to ingest large amounts of food during laying.

Incubation period

Food consumption by pairs on the four main treatments was not affected by diet treatment ($F = 0.88$, DF = 3,18; $P = 0.471$), but was affected by stage of incubation ($F = 2.82$, DF = 3,54; $P = 0.05$) (Fig. II-5). Food consumption per pair remained relatively stable through the first 3 wk of incubation, but then increased slightly in the final week (Fig. II-5), presumably reflecting increased food intake by females as their body reserves became depleted.

Females on the four main diet treatments lost progressively less

Table II-7: Laying characteristics of Canada geese in 1985.

Diet[1]	N	Egg weight[2] mean ± SD	Clutch size mean ± SD	Laying rate (d/egg) mean ± SD	Clutch weight mean ± SD
Control	7	158.7 ± 12.7	6.0 ± 0.8	1.57 ± 0.11	953.3 ± 155.7
Low availability	5	157.0 ± 5.9	5.4 ± 0.9	1.64 ± 0.07	851.8 ± 165.7
Reass. to control	6	159.0 ± 11.5	5.7 ± 1.2	1.59 ± 0.15	904.7 ± 171.5
Reass. to corn	5	157.5 ± 8.0	5.8 ± 0.4	1.54 ± 0.09	915.3 ± 105.6
Alfalfa	1	134.5	4.0	1.67	538.0

[1] The first four diets were compared by analysis of covariance (the covariate being the same characteristic from the previous year). These four diets did not significantly affect any of the characteristics. A t-test was used to compare differences (between values for 1984 and 1985) in characteristics of the female nesting on the alfalfa treatment with those of females on the control diet. All characteristics were affected (see text).

[2] Mean of the mean egg weight from each clutch.

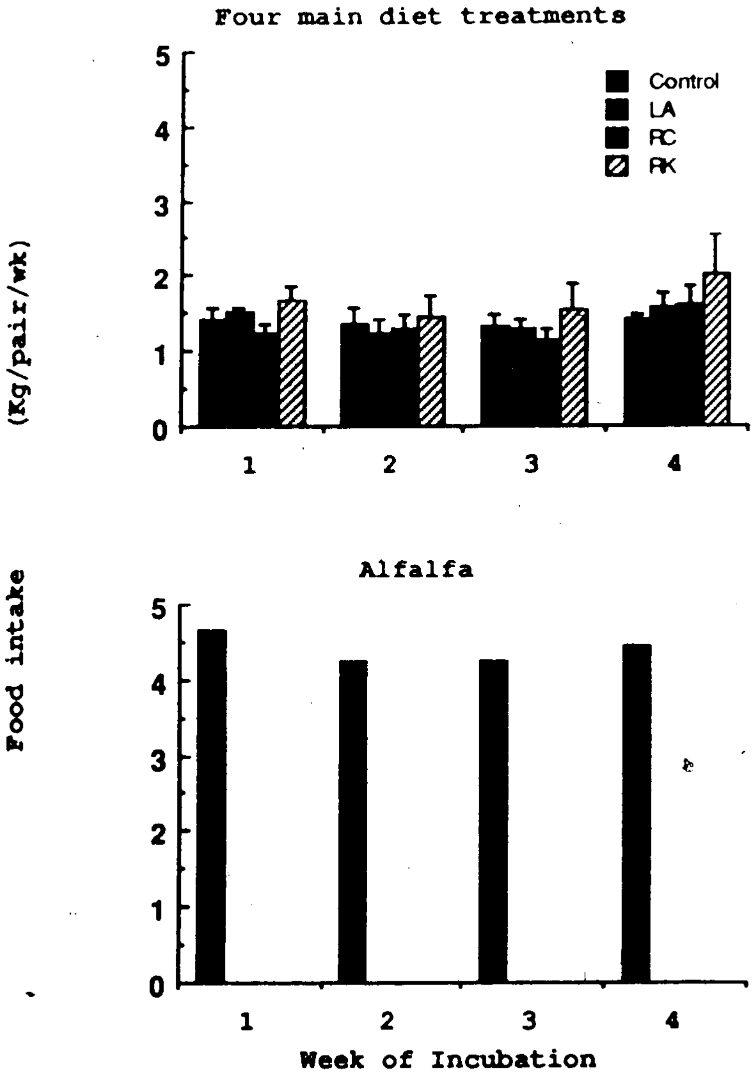

Fig. II-5: Food intake (mean ± SE) by Canada geese on the four main diet treatments and on the alfalfa diet (N = 1) over the period of incubation.

weight as incubation proceeded (Fig. II-6). A two way analysis of variance indicated that stage of incubation had a strong effect on weight loss by females (F = 13.55, DF = 2,38; P < 0.0001), but that diet treatments did not (F = 0.026, DF = 3,19; P = 0.8547).

By contrast, two-way analysis of variance indicated a significant effect of diet treatment on the weight dynamics of males (F = 7.83, DF = 3,17; P = 0.002), but no effect of week of incubation (F = 1.14, DF = 2,34; P = 0.331). During incubation, males on the RC and RK diets gained more weight (or lost less) than males on the control diet (Fig. II-7). This difference may have arisen from a continued attempt by reassigned males to regain weight they lost on their original diet treatments (Table II-5), or possibly from increased gut efficiency that resulted from preconditioning on the alfalfa diet.

While the single pair that reproduced on the alfalfa diet ate significantly more (all P values < 0.001) during all weeks of incubation than control pairs (Fig. II-5), this difference does not by itself indicate that the female of the pair was eating more than the females of other pairs. The difference could potentially be explained solely by the male's compensation (in the form of increased food consumption) for the lower digestible energy content of alfalfa. However, the weight dynamics of this female (Fig. II-6) suggest that she consumed more food than control females. This female lost significantly less weight during the first (t = 4.80; P = 0.003), and second (t = 11.93; P < 0.001) weeks of incubation than females on the control diet (Fig. II-6). These lower weight losses presumably indicated reduced contributions of body reserves to this female's energy requirements (nutrient requirements during incubation being primarily for energy; Raveling 1979). Hence, she must have relied more heavily on food to meet her energy demand. The alternative, substantial reduction of the energy requirement, is not possible since energy expenditure during normal incubation is already minimal (1.25 x BMR; Raveling 1979).

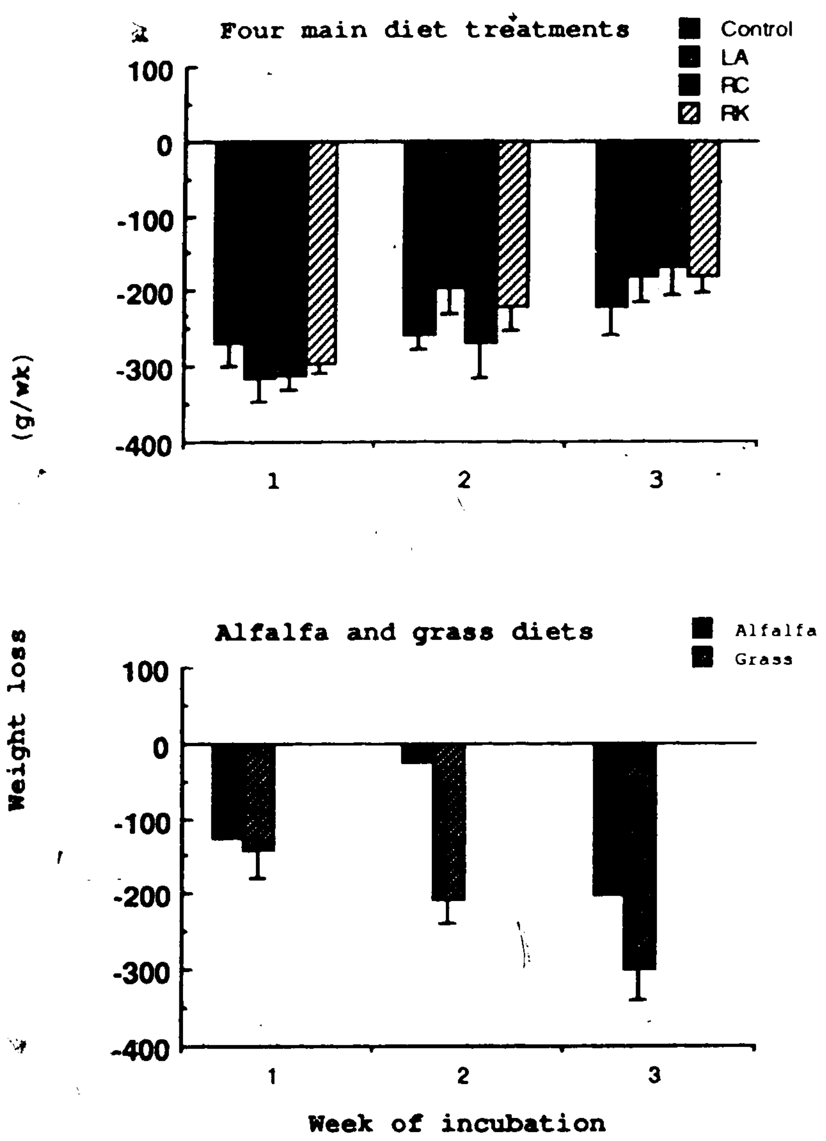

Fig. II-6: Weight loss (mean ± SE) by female Canada geese on the four main diet treatments, and on alfalfa and grass diets, over the incubation period beginning at Day 3.

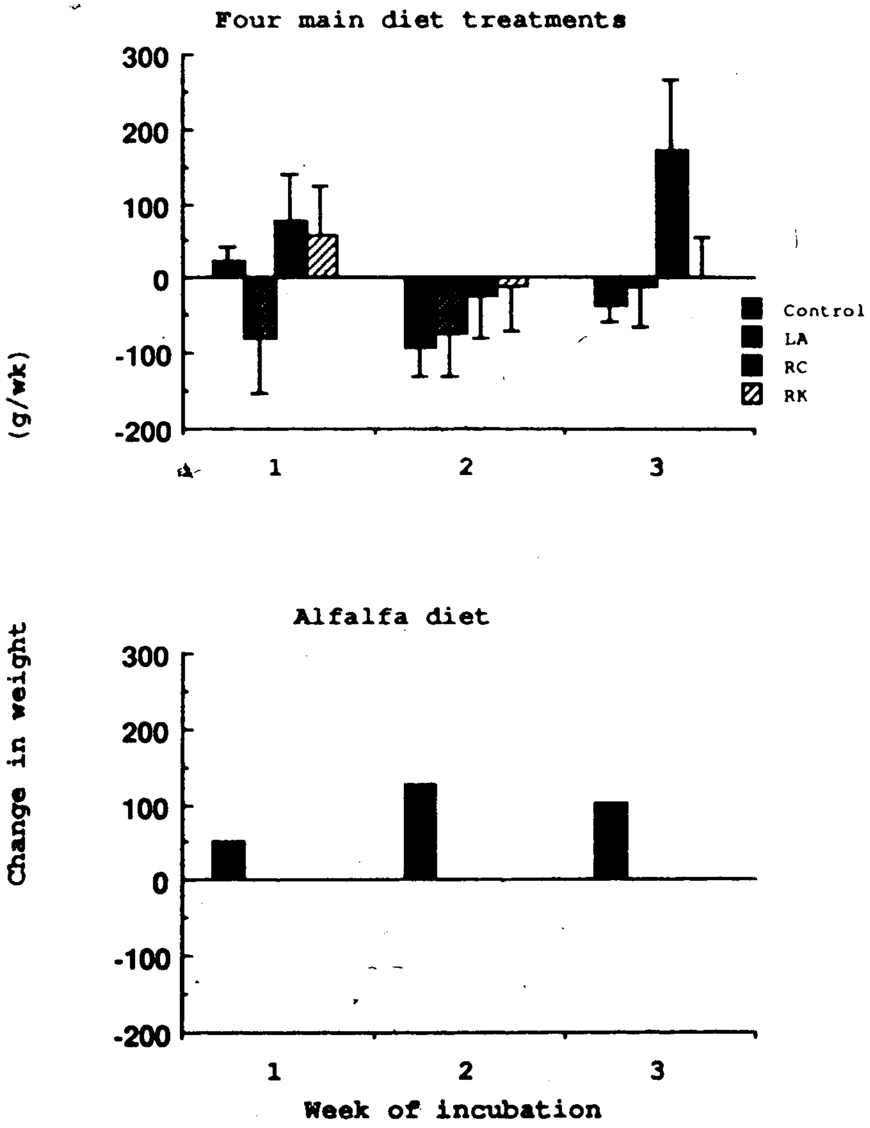

Fig. II-7: Changes in body weight (mean ± SE) among male Canada geese on the four main diet treatments, and on the alfalfa diet (N = 1), over the incubation period beginning at Day 3.

Food intake and weight dynamics-1986

Pre-laying and laying periods

Unusually warm temperatures in March of 1986 promoted early growth of grass. New shoots of crested wheatgrass (*Agropyron cristatum*) were evident throughout most of the grazing pen on April 2, 1986. A single 20 x 20 cm sample from the area of greatest abundance of new shoots indicated that there was approximately 40 g (dry weight)/m^2 of new wheatgrass growth. The biomass of green vegetation throughout the pen was equal to, or greater than this throughout the experiment (Table II-8). Protein content of this vegetation declined as the season progressed but never fell below 14%. Fiber and lignin concentrations were largely stable and relatively low throughout the course of the experiment, suggesting that the digestibility of this vegetation could be quite high.

Females and males devoted 70 and 51%, respectively, of their time to feeding during the first week they were in the grazing pen (Table II-9). This resulted in both sexes recovering rapidly weight they had lost during food restriction. Females regained 191 ± 78 g of 314 ± 229 g lost during the diet restriction. Males gained even more weight, on average, than they had lost during food restriction (246 ± 238 g versus 194 ± 250 g). While these weight gains may in part reflect increased weight of ingesta in the guts of birds, it is unlikely that this explains very much of the weight gain, as the collection of the geese for weighing interfered with their foraging for a period of approximately 30-50 min prior to weighing and appeared to stimulate defecation during that time (personal observation).

Females spent significantly less of their available time (time when they were not on the nest) grazing during the rapid yolk deposition (RYD) and laying (LYG) periods (average of 53%) than they had during the first week they were in the grazing pen (70%; Table II-9). Approximately half of the reduction in time spent feeding was explained by an increase in time spent loafing (Table

Table II-8: Biomass and composition of crested wheatgrass (all above ground parts grown that season - dry weight basis).[1]

	Apr 02	Apr 07	Apr 20	Apr 27	May 04	May 10	May 17
Biomass (g/m^2)	40.0	67.5	42.5	60.0	55.0	57.5	42.5
Protein (%)		24.9	20.3	15.9	15.0	14.6	14.0
Fiber (%)		21.4	21.8	22.4	24.6	23.7	24.1
Lignin (%)		2.0	2.0	2.0	2.0	2.2	2.0

[1] On Apr 2 a single subsample (20 x 20 cm) was collected from the area of greatest apparent abundance. This sample did not provide enough vegetation for analysis. On the remaining dates, eight subsamples were collected and pooled to provide enough vegetation for analysis.

Table II-9: Behavior of paired Canada geese recovering from food restriction and subsequently producing eggs on grazed vegetation, mainly wheatgrass.[1] Values are mean (± SD) percentages.

		First week after food restriction (N = 24)[2]	Rapid yolk deposition (N = 28)[2]	Laying (N = 27)[2]
	Females	69.9 ± 16.0 a	50.2 ± 21.5 b	55.0 ± 18.1 b
Feeding		***	*	***
	Males	51.0 ± 15.9 a	38.8 ± 19.8 b	37.0 ± 15.2 b
	Females	11.9 ± 11.0	22.1 ± 23.4	18.8 ± 19.0
Loafing		**	NS	NS
	Males	5.3 ± 6.6 a	17.4 ± 21.6 b	13.3 ± 12.8 b
	Females	4.7 ± 6.4	5.9 ± 9.6	3.3 ± 6.1
Alert		***	***	***
	Males	29.3 ± 14.3	26.0 ± 18.0	33.8 ± 23.2
	Females	13.4 ± 12.1	21.7 ± 15.2	22.9 ± 15.4
Other		NS	NS	*
	Males	14.4 ± 13.6	17.8 ± 16.7	15.8 ± 13.6

[1] Letters (a and b) indicate significant differences based on an LSD range test for differences among the three periods. Letters are only provided if analysis of variance indicated there was a difference.

The behavior of pair members was compared within periods by paired t-tests.

NS $p > 0.05$
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

[2] Sample sizes are the number of observation bouts (15 scans per bout), not the number of pairs.

II-9). Hence, the decrease in time spent feeding was apparently not the result of competing demands for time to perform other activities.

In addition to the decline in time spent feeding, there appeared to be a decrease in feeding intensity. I did not count bites/min, but females did appear to be feeding far more rapidly before the RYD and LYG periods. Further, females that were forming eggs (RYD and LYG periods) were frequently observed "tasting" vegetation (squeezing the tips of grass blades between the mandibles and then releasing them) without eating them, but this behavior was not observed in males or in females that were not forming eggs.

Females grazing wheatgrass began laying at body weights that were on average 214 ± 238 g (N = 14) lighter than the corresponding weights when these females had access to concentrated foods. This difference in pre-laying weights combined with greater average weight loss during laying (Fig. II-4) produced post-laying female weights that were, on average, 290 ± 213 g (N = 12) less than they were in the previous year when on concentrated artificial foods.

The estimated dry matter intakes (based on fecal weights and defecation rates; see Appendix III) of females were 1.38 kg/wk during RYD and 1.07 kg/wk during LYG. Based on the digestible energy of the grass (Table II-2) these intakes would provide females with 2361 kcal/wk and 1831 kcal/wk. These energy values represent 76 and 62% of the maintenance energy requirements (2.0 x BMR for captive geese; Boudewijn 1984 - BMR calculated according to Aschoff and Pohl 1970) of females during the RYG (3104 kcal/wk) and LYG (2964 kcal/wk) periods.

Since the geese (both males and females) gained weight on grass initially, they must have been capable of processing more than enough vegetation to meet their maintenance energy requirements at that time. The apparent inability of females to process enough grass to meet their maintenance energy requirement during the RYD period suggests that the amount they could process decreased between the time they were first given access to the grazing pen and the RYD period. The decrease in estimated dry matter intake between the RYD and LYG periods (from 1.38 to 1.07 kg) suggests that the use of food by females was constrained even further during the LYG period.

Males also reduced the time they spent feeding and increased time spent loafing (Table II-9) between the first week of the experiment and the RYD and LYG periods. However, unlike females, males had recovered fully body weight lost during the food restriction. Hence, the reduction in the time that males spent feeding may not reflect a constraint on food intake. It may simply reflect the fact that males no longer required nutrients for the purpose of replenishing body reserves.

Incubation period

Females on the grass diet in 1986 lost less weight during the first week of incubation (Fig. II-6; paired-t = 3.32, two-tailed P = 0.007) than they had in the previous year when they had access to concentrated foods throughout the nesting cycle. This reduction in weight loss is attributed to the depletion of fat reserves during egg formation and consequent greater reliance on exogenous energy (food) in 1986; as I have already suggested for the female that nested on alfalfa pellets in 1985. During the second week of incubation females consuming grass lost roughly the same amount of weight as females using concentrated foods (Fig. II-6). In the third week of incubation they lost an average of 117.5 g more than they lost in the previous year when they nested on concentrated foods, a difference that was not quite significant (two-tailed P = 0.058). Females that incubated for 24 d were 307.5 ± 273.4 g (N = 10) lighter in 1986 than they were in the previous year when they had access to concentrated foods.

I was not able to compare weekly weight losses of males during incubation, but male body weights on Days 3 and 24 of incubation were similar between the two years (P = 0.373 and 0.276, respectively). Thus, it appears that males had no difficulty meeting their food requirements in the grazing pen.

Egg production and nest attentiveness

1984

Twenty-one of 23 pairs of Canada geese that had nested in 1983 produced at least one clutch in 1984. Eight pairs (predominately those that initiated their first clutch quite early) produced a second clutch. The mean interval between the removal of first clutches and the appearance of the first egg of second clutches was 15.1 ± 2.4 d. Since Canada geese require 13 d for follicle maturation (Bromley 1984), this interval suggests that the females did not need to replenish their body reserves before they reinitiated follicle maturation for the second clutch. Contrary to my predictions (Table II-1), the egg weights, clutch sizes, and laying rates for first and second clutches were similar (Table II-10).

1985

As predicted (Table II-1), the LA diet reduced the proportion of pairs that nested (Table II-6). This suggests that food availability (relative ease with which food can be obtained) influenced the female's physiological ability to nest. The alfalfa treatment (reduced food availability and lower energy content) reduced even further the proportion of pairs nesting (Table II-6), suggesting that energy content had an additional effect on the proportion of pairs that nested.

Females reassigned to the control and corn diets initiated clutches 10.9 ± 3.2 d (N = 11) after being reassigned. This indicates that despite their reduced body weights (Table II-5), females initiated follicle maturation as soon as they received an ad lib. supply of concentrated food.

Most of the variation in egg weight and clutch size is among rather than within females (Leblanc 1986). To control for this source of variation, I used egg weights (mean of each female's first clutch) and first clutch sizes from 1984 as covariates in analyses of covariance assessing the effects of the diet treatments on these characteristics in 1985. Contrary to my predictions (Table II-1), the four main diet treatments did not affect any of

Table II-10: Laying characteristics of Canada geese that produced two clutches in 1984.

N = 8	First clutch mean ± SD	Second clutch mean ± SD	Difference mean ± SD	paired-t	one-tailed p^1
Egg weight[2] (g)	168.5 ± 8.4	167.2 ± 7.8	1.3 ± 3.3	1.1	0.154
Clutch size	5.6 ± 0.9	5.6 ± 0.5	0.0 ± 1.2	0.0	1.000
Laying rate (d/egg)	1.6 ± 0.1	1.7 ± 0.2	0.1 ± 0.2	-0.3	0.395

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[1] Testing for smaller egg and clutch size and reduced laying rate (increased d/egg) because of reserve depletion after producing the first clutch.

[2] Mean of the mean egg weight from each clutch.

the variables: egg weight, clutch size, or laying rate (Table II-7).

However, the female that nested on the alfalfa diet laid eggs that were an average of 13.2% lighter than the eggs she produced the previous year (1984). T-tests comparing the change in egg weight (mean of the 1984 clutch minus the mean of the 1985 clutch - t = 7.75, DF = 5; one-tailed P = 0.001) and change in clutch size (t = 3.16, DF = 6; one tailed P = 0.008) of this female with changes observed in control females indicated significant differences. This female also produced eggs more slowly (greater mean number of d/egg) than females on the control diet (t = 2.10, DF = 6; one-tailed P = 0.041).

Diet treatments used in 1985 did not affect recess length, recess frequency (recesses/d), or the total time that females spent off the nest (results of analyses of covariance adjusting for differences in day of incubation; all P values > 0.21). Consequently, data from all treatments were pooled for further analysis. Day of incubation was not significantly correlated (all P values > 0.28) with recess length, recess frequency, or total recess time in this year.

As predicted (Table II-1), the four main diet treatments affected the number of eggs that failed to hatch (Kruskal-Wallis one-way ANOVA, P = 0.01). More eggs failed to hatch in the LA and RK treatments than in the control or the RC treatments (Table II-11). Since the incubation behavior of the females was not affected by the diet treatments, this increase in the number of eggs that failed to hatch may reflect differences in egg quality. The female that nested on the alfalfa diet hatched all four eggs laid (Table II-11).

1986

Of 16 adult female Canada geese that had nested in 1985 and were retained, 14 produced a clutch in 1986. This proportion was not significantly lower than the proportion of proven breeders that nested in 1984 (Table II-6).

Table II-11: The fate of Canada goose eggs from clutches produced on a variety of diet treatments: four main diet treatments (control, low food availability-LA, reassigned to control-RC, and reassigned to corn-RK), an alfalfa diet in 1985, and a wheatgrass diet in 1986.

Diet	# of clutches excluded from analysis[1]	# of eggs involved from each clutch			Mean # hatched/ clutch
		Depredated[2]	Failed to hatch	Hatched	
Control	1	0,0,0,0,0,0	1,1,0,0,0,1	4,6,6,7,6,4	5.50
LA	1	0,0,0,0	2,3,1,2	4,3,4,2	3.25
RC	2	0,0,0,0	1,0,0,1	5,5,7,4	5.25
RK	2	0,0,0	2,2,2	3,4,4	3.68
Alfalfa	0	0	0	4	4.00
Wheatgrass[3]	1	1,0,0,0,0,3,0, 0,0,0,0,0,0	0,0,0,4,0,4,1 4,2,0,4,0,1	4,5,6,0,4,0,4, 0,3,5,0,4,5	3.08

[1] Eggs that failed to hatch were opened and examined for embryonic development. There was no evidence of embryonic development in six of the clutches produced in 1985, suggesting that the entire clutch was infertile. These clutches and one of the clutches produced in 1986 (by a hen without a mate, that was prevented from incubating her clutch by a neighboring pair) were excluded from the analysis.

[2] The chain link fence and screen roof enclosing the breeding pens excluded egg predators entirely in 1985.

[3] Underlined values indicate clutches deserted before Day 24 of incubation.

Egg weight, clutch weight, and laying rate of Canada geese were all reduced when the geese nested on a diet of wheatgrass (Table II-12). Laying females lost slightly more weight when they nested on the grass diet than when they nested on concentrated foods (Fig. II-4). Hence, their body reserves (endogenous nutrients) contributed presumably as much or more to the formation of eggs when they nested on a grass diet than when they nested on a diet of concentrated artificial foods. This suggests that the wheatgrass (exogenous nutrient source) was not adequate to realize the full potential of clutch and egg sizes recorded from these birds on the artificial and somewhat more nutritious control diet. Since the amount of grass available for the geese appeared abundant throughout the experiment (Table II-8) and its consumption was not limited by time available for grazing (Table II-9), any potential deficiencies in this diet must have arisen from its quality (in conjunction with the ability of the females to process it in sufficient amounts) rather than its quantity. Quality of the grass was quite good (high protein content and low fiber and lignin contents; Table II-8) throughout the experiment, which suggests that to achieve their potential egg and clutch sizes, females require extremely high quality vegetation during laying, or that lack of conditioning of their guts to grazed vegetation before their release into the grazing pen reduced their ability to acquire necessary nutrients.

One female (without a gander) was repeatedly driven from her nest by a pair that had not yet nested. Three other females began incubating but deserted their clutches before Day 24 of incubation. These females were excluded from analysis.

Females were significantly less attentive to their clutches in 1986 when in the grazing pen than in 1985 when in individual breeding pens (Table II-13). This reduction in nest attentiveness was the result of a combination of increased recess length and frequency. Recess frequency was not significantly correlated with day of incubation, but recess length was ($r = 0.3622$, $n = 42$; $P = 0.009$).

Table II-12: Laying characteristics (mean ± SD) of the same 14 female Canada geese producing a clutch of eggs on concentrated foods in 1985[1] and grazed wheatgrass in 1986.

Variable	Concentrated foods	Grazed wheatgrass	Difference	paired t	one-tailed P[2]
Egg weight[3] (g)	161.8 ± 9.9	155.7 ± 8.0	-6.1 ± 5.4	-4.3	0.001
Clutch size	5.7 ± 0.7	4.9 ± 0.9	-0.8 ± 1.2	-2.5	0.014
Laying rate (d/egg)	1.6 ± 0.3	1.8 ± 0.3	0.2 ± 0.4	2.4	0.016

[1] Data from 1984 were substituted for the single female that used alfalfa (not a concentrated diet) in 1985.

[2] Testing for smaller egg and clutch size and reduced laying rate (increased d/egg) because of lower energy content in grass.

[3] Mean egg weight refers to the mean of the mean egg weight from each clutch.

Table II-13: Incubation behavior of Canada geese on diets of either concentrated foods (control, RC and RK diets) or wheatgrass.[1]

Diet	# nest-days	Modal recess length (min)	Mean recess length (min)	Mean recesses/ day	Mean recess time/d (min)	Attentive-ness (mean % of 24 h period)[2]
Concentrates (1985)	69	6	13.2 (8.7)	2.8 (3.6)	35.8 (37.5)	97.5 (2.6)
P value[3]		-	< 0.001	0.010	< 0.001	< 0.001
Wheatgrass (1986)	43	18	23.0 (10.8)	4.2 (3.2)	107.1 (81.7)	92.6 (5.7)

[1] Adjusted (analysis of covariance) means are presented with standard deviations in ( ).

[2] Attentiveness was only monitored during the daylight period and it was assumed that females only left nests during daylight. The mean lengths of the periods monitored averaged 667 and 716 min/day for 1985 and 1986, respectively.

[3] From analyses of covariance correcting for differences in day of incubation.

The proportion of time that females spent feeding while they were on incubation recesses in 1986 (64.3 ± 32.2%; N = 100) was not significantly correlated with day of incubation (r = -0.1223, N = 100; P = 0.114).

Fewer goslings hatched from clutches produced and incubated in the grazing pen than from control clutches produced and incubated in small breeding pens (Kruskal-Wallis one-way ANOVA, P = 0.0216; Table II-11). However, this difference was largely the result of total clutch losses by three females that deserted their clutches before Day 24 of incubation, and to a lesser extent, to the reduced clutch size in the grazing pen (Table II-12). Despite reduced nest attentiveness by females incubating in the grazing pen (Table II-13), the number of eggs that failed to hatch from clutches there (Table II-11) was not significantly different from the numbers that failed to hatch from clutches produced and incubated by females on the control diet in 1985 (Kruskal-Wallis one-way ANOVA, P = 0.3970).

Discussion

Egg production

Vermeer (1970) reported that the mean clutch sizes of wild geese at two locations near Brooks were 5.41 and 5.80. These values are not different from the mean clutch size of captive geese provided with an ad lib. supply of concentrated food (5.7 eggs; Table II-12), but are considerably (and at one location significantly) greater than the mean clutch size of the captive geese when they were restricted to an abundant supply of grass during nesting (4.9 eggs; Table II-12).

Kossack (1950), Brakhage (1965) and Cooper (1978) reported an inter-egg interval of approximately 1.5 d for Canada geese. When captive geese received an ad lib. supply of concentrated food the inter-egg interval was only slightly greater (1.6 d) than the interval reported for wild geese, but this interval was significantly longer when captive females were restricted to a diet of grazed wheatgrass (1.8 d).

While egg size and clutch size were both reduced when geese were restricted to alfalfa pellets and to grazed wheatgrass, the proportional decrease in egg size (3.8%) was much less than the decrease in clutch size (14.0%). This supports Ricklef's (1974) suggestion that egg size tends to be maintained at the expense of clutch size.

In this study females with previous breeding experience and access to concentrated food during egg formation always produced clutches of at least five eggs (even if their body weights, and presumably their body reserves, were considerably reduced just prior to egg formation). However, the female that nested on a diet of alfalfa pellets in 1985 and several females that nested on a diet of wheatgrass in 1986 produced four-egg clutches despite previous breeding experience. Aldrich (1983) reported that experienced female *B. c. moffitti* in his study always produced clutches of at least five eggs while inexperienced females produced clutches of four eggs. Aldrich attributed the difference in clutch size to an apparent difference in the abilities of the two groups to acquire pre-laying body reserves. Inexperienced breeders finished laying an average of 339 g lighter than experienced breeders (despite being full grown and at least 4 y old). Aldrich suggested that this difference in post-laying weights resulted from either lower winter weights or reduced weight gain before onset of reproduction.

This study confirmed that four-egg clutches are associated with lower post-laying weights independent of breeding experience. However, differences in exogenous nutrient acquisition during the period of egg formation (imposed by diet treatments), rather than differences in pre-breeding (prior to the initiation of follicle maturation) weights seemed to explain the difference in post-laying weight and clutch size recorded. This suggests that differences between experienced and inexperienced females may result from differences in their abilities to acquire exogenous nutrients during egg formation in addition to any differences that may exist prior to follicle maturation.

Incubation

The nest attentiveness of female *B. c. moffitti* provided with an ad lib. supply of concentrated foods (97.5%; Table II-13) was the same as recorded by Aldrich (1983) in a study of this subspecies in California. However, when these same females began incubation at lower body weights in 1986, when on a diet of grazed wheatgrass, they showed lower nest attentiveness than most geese studied to date (see Thompson and Raveling 1987 for review). Aldrich (1983) and Bromley (1984) reported substantial decreases in nest attentiveness toward the end of the incubation period, but this is the first report of markedly decreased attentiveness in early incubation. It provides strong evidence that declining body reserves are indeed the cause of decreasing nest attentiveness.

Agonistic interactions between ganders were infrequent and restricted to territorial boundaries, and did not appear to influence the behavior of incubating females. Females (with the exception of one unpaired female) were never driven from their nests by other geese.

The weight losses of incubating *B. c. moffitti* females that nested on concentrated diets (breeder pellets or corn) followed the same pattern that Aldrich (1983) reported for this subspecies on a high quality diet. The rate of weight loss decreased as incubation progressed. However, this pattern was not observed in females that began incubation at reduced body weights (those nesting on a diet of alfalfa pellets or grazed wheatgrass). These females exhibited reduced weight loss during early incubation relative to those that began incubation at higher body weights, suggesting that reduced nest attentiveness allowed them to compensate for lower energy reserves, presumably by consuming more food while they were away from the nest.

Greater weight loss at the end than at the beginning of the incubation period may reflect increased reliance on protein catabolism to meet energy demands after fat stores were depleted, as reported for lesser snow geese (*Chen caerulescens caerulescens;* Ankney and MacInnes 1978). On Day 24 of incubation, the mean body weight of captive females grazing wheatgrass (3065 ± 190 g) was 121 g lighter than the corresponding weight of wild females at the same stage of incubation, that contained an average of only 65 g of fat (see Chapter III - Table III-2); suggesting that captive females had, in all probability, depleted their fat reserves. Protein catabolism produces less than half the energy of fat catabolism, and protein is stored in conjunction with water but fat is not (Ricklefs 1974). Hence, protein use produces greater weight loss than fat use in providing a given unit of energy.

Harvey (1971) and MacInnes et al. (1974) reported that reduced nest attentiveness lowered the hatchability of goose eggs. However, reduced nest attentiveness of captive females grazing on wheatgrass (Table II-13) did not increase significantly the number of eggs failing to hatch in 1986 (Table II-11). Unusually warm weather in this year may explain the high rates of embryo survival in this situation despite reduced nest attentiveness. Only 6% of eggs produced in the grazing pen were lost to predators, probably as a result of reduced predation within the Brooks Wildlife Center.

Food use by laying females

Geese normally compensate for the relatively low energy content of their grass diet by processing large volumes of food (Sibly 1981). However, this tactic doesn't appear to be acceptable to laying females. Mainguy and Thomas (1985) reported that an apparent increase in food availability did not reduce the use of body reserves by laying female *B. c. maxima* or increase the weight of clutches produced by them. Presumably then, the increase in food availability did not prompt these females to use more of it because some other factor was constraining its use. Further, Bromley (1984) calculated that female *B. c. occidentalis* derived 140 kcal less energy from their daily food intake during the laying than during the pre-laying period. This decrease occurred despite an apparent increase in food availability, suggesting that the ingestion of food by these females was also internally constrained during laying.

This study provided additional evidence that the use of food by laying Canada geese was internally constrained at a reduced level during laying. Females lost > 700 g of body weight during laying despite an ad lib. supply of breeder pellets enriched in amino acids required for egg production (Fig. II-4; control and RC diets). Pairs with reduced body weights (and presumably reduced body reserves) consumed additional food (relative to pairs, the weights of which were not reduced) before, but not during the laying period (Table II-3, Fig. II-2). Additionally, the estimated dry matter intake of females grazing on wheatgrass was only 1.07 kg/wk, a value that supplied only 62% of their maintenance energy requirement.

A number of authors have demonstrated that captivity and the use of low fiber diets reduce the size and capacity of the gut (see Sibly 1981 and Buchsbaum et al. 1986 for reviews). However, Buchsbaum et al. (1986) reported that captivity and very limited exposure to natural food items did not reduce the ability of Canada geese to digest herbage. Hence, it seems unlikely that the failure of the females to ingest enough of the wheatgrass to meet even their maintenance energy requirement during laying was simply the result of poorly adapted guts. The ability of females to increase their body weights in the first week of the experiment suggested that they were able to digest the wheatgrass effectively, and to obtain more than their maintenance energy requirement from the wheatgrass at that time. However, the digestibility of the wheatgrass may have declined between the first week of the experiment and laying.

Since the mean post-laying body weight of these females (3683 ± 339 g) was 135 g less than the mean post-laying weight recorded in wild females (Chapter III, Table III-2), abnormally high body reserves (obesity) is not a tenable explanation for the low dry matter intake of these females. Anorexia is not a potential explanation either, since laying females devoted 55% of the diurnal period to feeding (Table II-9). Likewise, food availability can not explain the low level of food consumed by these females, since wheatgrass remained abundant throughout the experiment (Table II-

8).

Buchsbaum et al. (1986) reported that palatability reducing phenols in plants result in the production of secondary metabolites that interfere with protein absorption from the gut. Perhaps these secondary metabolites have the potential to interfere with protein metabolism at other sites. If this is true, then protein metabolism associated with egg formation (especially albumin secretion which occurs very rapidly) may require laying females to reduce their food intake in order to minimize the levels of these secondary metabolites in their blood streams. These secondary metabolites might also interfere with enzymatic activity necessary to produce linoleic acid (which occurs in eggs at much higher concentrations than in grass; McLandress and Raveling 1981)

Very selective foraging, including rejection of particular grass blades by laying females (personal observation) suggested that they may have been attempting to minimize ingestion of deleterious plant constituents, consistent with the idea that the laying process requires physiological conditions that require reduced food use.

Wild geese nesting near Brooks produced larger clutches and were more attentive to those clutches (Chapter III) than captive females grazing on an abundant supply of wheatgrass. Since higher nest attentiveness seems to reflect larger body reserves (Aldrich and Raveling 1983), wild females may have been able to derive more energy from the wild food resource than captive females (with possibly less well adapted guts) derived from the abundant supply of wheatgrass. While wild females may have brought larger reserves to their breeding grounds than captive females brought to the wheatgrass situation, wild females could only have maintained those reserves if they either encountered a higher quality food source on the breeding grounds between arrival and laying (a period of 3 wk; Ewaschuk 1970), or if they had better adapted guts, or both.

Two factors may have reduced the digestibility of the wheatgrass used by the captive females. First, an unusually warm spring in the year of study advanced the development of the grass. Since digestibility declines with increasing plant maturity (Van Soest 1969), the wheatgrass may not have been as digestible as the herbage used by wild females (which responded to the unusually warm spring by nesting earlier than normal). Second, the wheatgrass was intensively grazed by the geese before they began laying. Presumably, the geese removed the most digestible succulent new growth first. Hence, the digestibility of the wild food resource (which was presumably not exposed to such intensive grazing) may have been higher than that of the wheatgrass.

While these factors may have reduced the quality (digestible energy and/or palatability) of the wheatgrass, samples indicated that the wheatgrass was still of good quality (Table II-8: high protein and low fiber and lignin content). Hence, reductions in egg size and number, and nest attentiveness that were recorded in this situation suggest that female *B. c. moffitti* require herbage of extremely high quality during laying (or perhaps very well adapted guts) in order to realize their potential egg and clutch sizes, and to retain body reserves after laying that allow them to maintain high nest attentiveness.

Timing of Reproduction

Barry (1962) observed that arctic nesting geese delayed nesting in years of delayed snowmelt. Barry attributed delays to the absence of suitable nesting sites, but Hamann et al. (1986) reported delays in arctic nesting snow geese (*Chen caerulescens*), despite the availability of nesting sites. This latter observation suggests that some additional factor (perhaps adequacy of the food resource on the breeding grounds) is involved in nesting delays. In this study reduced food availability reduced the proportion of pairs that nested initially (Table II-6), suggesting that food availability has an influence on the ability of geese to produce a clutch. Hanson (1962) and Raveling and Lumsden (1977) suggested that food was not available to Canada geese nesting in the arctic until after laying was complete, but this suggestion has subsequently been questioned (Bromley 1984). It is possible that the correlation between snowmelt and nesting dates arises from the impact of snow cover on food availability on the breeding grounds rather than availibility of nesting sites.

Many investigators have suggested that the nutritional status of laying females is compromised by the need to begin nesting before food is abundant on the breeding grounds so that subsequent events (eg. depletion of energy reserves that support incubation - Bromley 1984; hatch of the clutch - Harvey 1971; or growth and fledging of goslings - Barry 1962, Newton and Kerbes 1974, Sedinger and Raveling 1984) are optimally timed. However, given the apparent constraint on the amount of food that laying females use, the adequacy of the food resource for laying females is probably a function of the digestibility of food rather that its abundance (above a very low level). McLandress and Raveling (1981) suggested that extremely high quality of new growth grass immediately after snowmelt was critical for the accumulation of body reserves by *B. c. maxima* on wintering grounds. This resource may also be important in allowing laying females to acquire nutrients they need for the realization of potential egg and clutch size. Hence, the nutritional status of females may not be compromised by early nesting. On the contrary, early nesting may enhance the nutritional status of females since it synchronizes the laying period with the period of highest forage digestibility (Van Soest 1969).

In sum, food availability influences the female's ability to initiate follicle maturation, but high food abundance during laying is of little value since females are apparently unwilling or unable to ingest large quantities of food at that time. High digestible energy content (and possibly low levels of phenols that reduce palatability) in the diet of laying females appear(s) to be essential in allowing western Canada goose females to realize their potential egg and clutch sizes and still maintain energy reserves that allow them to maintain high nest attentiveness during incubation.

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III. FOOD AND BODY RESERVE USE DURING INCUBATION

Introduction

Female Canada geese (*Branta canadensis*) incubate their clutches without assistance from the male. High levels of incubation attentiveness are essential to ensure maximum reproductive success. Absence from the nest results in higher rates of egg predation (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977) and may interfere with normal embryonic development (Harvey 1971, MacInnes et al. 1974, Aldrich 1983). The high levels of attentiveness, typical of Canada geese (Cooper 1978, Aldrich 1983, Bromley 1984), reduce significantly the time that females can spend feeding. Incubating females reconcile the time constraints of incubation with their own nutrient demands by catabolizing body reserves during incubation. This use of body reserves is controlled at the ultimate level by the trade off between increased fecundity in one year and continued survival of the goose (Aldrich 1983, Thompson and Raveling 1987). At the proximate level it is controlled by a genetically programmed reduction in the set point for body weight (or some component of it; Sherry et al. 1980). The set point for body weight is the weight below which physiological and behavioral reactions will intervene to maintain that weight.

The use of body reserves appears to vary considerably among subspecies of Canada geese. Raveling (1979) estimated that female cackling Canada geese (*B. c. minima*) derived less than half (48%) of their energy requirements from body reserves during incubation, while Bromley (1984) estimated that female dusky Canada geese (*B. c. occidentalis*) derived 66% of their incubation energy requirement from body reserves. Data supplied by Mainguy and Thomas (1985) indicate that female giant Canada geese (*B. c. maxima*) rely even more heavily on body reserves during incubation. By my calculations, using data from Tables 2 and 7 in Mainguy and Thomas (1985), giant females derive 72% of their incubation energy requirement from body reserves.

These differences are consistent with the trend towards increasing reliance on body reserves with increasing body size that was noted by Thompson and Raveling (1987). In an interspecific comparison, Thompson and Raveling (1987) reported an exception to this trend that they attributed largely to differences in the abilities of species to repel egg predators, but they noted that other factors might be involved. The wide range of body sizes among subspecies of the Canada goose provides an excellent opportunity to minimize confounding genotypic influences and examine the relationship between body size and the use of body reserves during incubation.

There is a progressive decline in rate of weight loss as incubation progresses in all subspecies of Canada geese studied to date (Cooper 1978, Aldrich 1983, Bromley 1984). Some of this change in rate of weight loss must result from decreased metabolic requirements associated with progressively lower body weights (Owen 1980), and decreased thermal stress associated with increasing ambient temperatures over the period of incubation (Aldrich 1983). However, behavioral changes concurrent with the change in the rate of weight loss suggest that increased reliance on direct food intake also contributes to the decline in rate of weight loss (and presumed use of body reserves). Cooper (1978), Aldrich (1983), and Bromley (1984) all observed decreases over the period of incubation in attentiveness of incubating Canada geese. Aldrich (1983) also reported that the proportion of time females (both cackling and western subspecies) devoted to feeding while they were off their nests increased in late incubation.

Raveling (1979) and Bromley (1984) calculated the energy contributed by food intake by subtracting the energy derived from the use of body reserves over the course of the incubation period from the estimated energy requirement for the entire incubation period. This method, however, only estimates the average contribution of food intake. If food intake increases as incubation progresses, then average values would overestimate the energy contribution from food intake in early incubation and underestimate it late in incubation.

Geese normally process large quantities of food very rapidly; this means that the time interval between ingestion and expulsion (in the form of feces) is normally quite short (1-2 h; Ebbinge et al. 1975, Owen 1975 and others). However, incubating female geese do not defecate on the nest. Instead, they retain undigested food until they leave their nest on their next incubation recess (Owen 1980). Since the normal throughput time (time elapsed between ingestion and defecation) is much greater than the length of a single recess and much less than the interval between incubation recesses (Cooper 1978, Aldrich 1983, Bromley 1984), incubating females probably retain all of the ingesta (except the portion absorbed by the gut) gathered during their last recess and no ingesta from previous recesses. Correcting for this absorption should allow one to estimate the total weight of food ingested on the previous recess from that remaining in the gut. Energy available to the goose from that food can then also be estimated.

The objectives of this study were to estimate the contributions that body reserves and direct food intake make to the energy budget of western Canada geese nesting on the Canadian prairies. I calculated the average contribution of body reserves over most (21 d) of the incubation period, and estimated the average contribution of food by subtraction. Since females of the western subspecies are intermediate in size between females of the dusky and giant subspecies, I predicted that they would also be intermediate in the extent to which they relied on body reserves during incubation.

I also calculated the energy that females derived from food ingested during a single incubation recess in the first and final weeks of incubation. Incubation rhythms of five females were determined in an effort to measure the number of recesses taken per d. This allowed me to estimate the extent of food use at these particular times as opposed to the average use over the entire incubation period and to assess variation among individuals at the same stage of incubation.

METHODS

Searches for nests of wild Canada geese were conducted on islands at Gleddie Lake (GL) and Rolling Hills Lake (RHL) near Brooks, Alberta (see Leblanc 1986 for a description of these areas) during 1985 and 1986. Initial searches were conducted at GL on April 5 (1985) and March 30 (1986), and at RHR on April 8 (1985) and April 1 (1986). The interval between searches varied from 2-4 d. Those nests found were observed during laying in order to establish when females began incubation. Eggs in each nest found were individually identified by nest and egg number (sequence within the clutch) using a waterproof felt marker. Nest locations were recorded on maps to facilitate their relocation during subsequent searches. The length and breadth of each egg was measured to the nearest 0.1 mm with Vernier calipers. These measurements were used to aid the identification of possible nest parasitism and to estimate fresh egg and clutch weights of females that were subsequently collected.

Incubating females were shot from nests that had been found during these nest searches. In 1985, females were collected from both GL and RHL. In 1986, collections were only made at RHL. One group of females was collected at approximately Day 3 of incubation and another group was collected at approximately Day 24 of incubation. The geese collected at these times are referred to as post-laying and pre-hatch females.

In an effort to obtain a representative and a homogeneous sample, I collected only females that had initiated their clutches within 4 d of the peak of nest initiation. The first day of incubation was defined as the day the clutch was completed. This date was predicted based upon the number of eggs in the nest on the previous visit, the mean clutch size of the population and the observed laying rate (taken from Cooper 1978). Nests were not visited for several days before collection in order to minimize disturbance. The number of eggs actually laid in a given nest and hatching dates were used to refine estimates of stage of incubation at the time of collection.

Collections were always performed in late afternoon and were accomplished in < 3 h on a single day (with one exception). Most of the geese were shot very near their nests and were recovered before they could reach the water's edge, but a few individuals either fell directly into water or were able to reach the water while wounded. All of these birds were towel dried before any measurements were taken.

Geese were weighed (to the nearest 25 g), measured (see Chapter IV for details), sealed inside two plastic bags, and placed in a freezer within 3 h of collection. They were later thawed, and reweighed to the nearest 1.0 g Remiges and retrices were removed and the birds were skinned and dissected. The abdominal cavity was opened and the gut (esophagus to cloaca inclusive) was removed. Intestinal mesenteries were severed and the length of the small intestine was measured in the manner outlined by Ankney (1977). Ingesta from the esophagus and proventriculus, the small intestine, and the large intestine and cloaca were gently expressed from these organs and weighed separately. The small intestine was severed immediately anterior and posterior to concentrations of ingesta to minimize the inclusion of endogenously derived material (mucous). Grasses from the esophagi of collected geese were identified according to Looman (1982).

The ventriculus was excised, weighed, opened, washed thoroughly, towel dried, and reweighed. The difference between the gross and net weights of the ventriculus was taken as the weight of the grit and food in the ventriculus.

Soft tissue was removed (as completely as possible) from each skeleton and recombined with the skin and digestive organs. This material (the bone-free carcass) was then sealed in an individually marked plastic bag and immediately refrozen. After selected measurements were taken (see Chapter IV) the skeletons were prepared by the staff of the Alberta Provincial Museum and Archives and deposited therein.

The bone-free carcasses were homogenized in a commercial meat grinder (Butcher Boy TCA 22 - 1.5 horsepower). Carcasses were passed through the grinder five times and the material was mixed thoroughly between grindings. Four replicate 30 g samples were removed from the resulting homogenate and immediately refrozen. Two of these samples were later weighed, oven dried (56^{o} C) to constant weight, reweighed, and further homogenized with a mortar and pestle. Three-g samples of this homogenate were subjected to fat extraction (4 h - using petroleum ether in a Soxhlet apparatus). If these two replicates agreed within 1.5%, the mean of the fat content of these two replicates was used to calculate the carcass fat content. Otherwise, two additional replicates were analyzed, and the mean of the pair of replicates that agreed most closely was used (maximum difference was 1.8%).

The weights of remiges and retrices, and wet weight of all ingesta plus estimated grit weight were subtracted from the thawed goose weight to give analyzed carcass weight. Analyzed carcass weight was multiplied by the proportional dry matter content (mean of two replicates) to calculate dry weight of the carcass. Total fat weight was calculated by mutiplying dry weight of the carcass by fat content (mean proportion of two replicates) of samples subjected to fat extraction. Campbell and Leatherland (1980) equations were used to calculate the protein content of carcasses. A water:nitrogen ratio of 18.1:1, and a protein:nitrogen ratio of 6.25:1 were used in these calculations. I did not attempt to measure carbohydrates (primarily glycogen) because their biomass is negligible in birds (Ricklefs 1974).

Basal metabolic rate (BMR) in kcal/d was calculated as 73.5 X (weight in kg.$^{0.734}$) (Aschoff and Pohl 1970). I used the average of the post-laying and pre-hatch weights in this calculation. I followed the procedures of Raveling (1979) to estimate the cost of incubation (1.25 X BMR), and to estimate the energy that females could derive from the catabolism of body reserves. The caloric yield of fat was taken to be 9.0 kcal/g and that of protein, 4.3 kcal/g.

Ingesta were oven dried (56^{o} C) to constant weight. Since the mean length of incubation bouts (Cooper 1978, Aldrich 1983) is considerably longer than the average passage rate of ingesta through geese (Ebbinge et al. 1975, Owen 1975 and others), I assumed that all ingesta within a goose's gut had been collected on that female's last incubation recess before her collection. Since incubating females do not defecate at their nests I assumed that the guts of incubating females contained all of the food that had been ingested on the previous recess except for the portion that had been absorbed through the wall of the gut. It was not always possible to observe females continuously from the time they flushed until they were recovered. Hence, it is conceivable that defecation may have occurred during collection. However, I believe that this possibility is unlikely because defecation was never observed during collection, and feces were found in cloacae of several females.

Dry weights of ingesta from the large intestine and the cloaca were multiplied by a factor of 1.67 to correct for absorption of dry matter that had presumably taken place. This correction factor corresponds to the 40% retention rate (digestibility) that Owen (1980) suggested for geese using new growth grasses. It is the inverse of the undigested portion of ingested food $(1/(1.0 - 0.4) = 1.67)$. I did not correct the weight of ingesta from the small intestine for absorption. While some absorption undoubtedly occurred I believe that the effect of this absorption was minimal and it may have been offset to some extent by the inclusion of some endogenously derived material (mucous) with ingesta. I used the total energy content of very young prairie grasses (4.28 kcal/g; Coupland 1973) and the retention rate (0.40) suggested by Owen (1980) to estimate the energy that geese could obtain from ingesta.

Egg measurements were used to calculate indices of egg volume according to the formula: volume index = length x breadth^2. This formula accounts for 91.6% of the variation in egg weight of western Canada geese (Leblanc 1986). Fresh egg weights were calculated using the equation: egg weight in g = (0.537 X egg volume) + 8.797 (Leblanc 1986). The calculated fresh weights of all eggs in a clutch were summed to provide estimates of fresh clutch weights. All clutches in which eggs were added at a rate of more than one per day and/or in which eggs of markedly different size or shape were found were considered parasitized and were excluded from analyses.

Incubation rhythms were monitored with super-eight movie cameras that exposed one frame per min. The cameras were housed in adapted ammunition boxes that were placed on the ground, and were concealed in natural vegetation 2-5 m from nests. Aldrich and Raveling (1983) reported that in a population of western Canada geese that they studied inexperienced breeders laid clutches of four eggs, while experienced breeders produced clutches of five or more eggs. Aldrich and Raveling (1983) also reported that the lower body reserves of inexperienced breeders relative to experienced breeders caused reduced nest attentiveness among inexperienced breeders during the final week of incubation. I monitored incubation rhythms at two nests that contained four eggs and at three nests that contained five or more eggs in order to contrast the behavior of assumed experienced and inexperienced breeders.

I attempted to observe with a 20X spotting scope the behavior of females during incubation recesses. I observed several females concurrently as long as they were on their nests and then focused exclusively on the first female that left her nest. Twenty-one h of observations were recorded, and 12 recesses were observed. Unfortunately, dense cattails and undulating topography prevented, in most instances, constant observation of females throughout the entire recess. Uninterrupted observation of females from the time they left their nests until they returned was accomplished only four times.

Statistical Methods

All statistical procedures were performed with the SPSSx statistical package. A probability level of 0.05 was used to evaluate statistical tests. One-tailed tests were used whenever consistent results from previous studies allowed me to predict the direction of potential differences. Means are reported ± standard deviations.

RESULTS

[illegible] post-laying and 12 pre hatch females were collected ([illegible]able III[illegible]). All post-laying females were collected 2-5 d after they began incubation. All pre-hatch females were collected in the final week of incubation.

Carcass Composition

The mean wet body weight of the sample of incubating females taken in the last week of incubation declined by 17% from that of the sample taken 3 wk earlier during the post-laying period (Table III-2). Most of the weight loss (71%) was the result of a marked decrease in fat content. Fat content declined by 87% during this period. Protein content also declined (Table III-2), but the change (6%) was minimal relative to that of fat.

Clutch Size and Weight

The clutches of three post-laying females and two pre-hatch females appeared to have been parasitized (Fig. III-1) based on differences in egg size and shape, or on laying rate (the addition of more than one egg per day). Consequently, for these females, I was unable to determine clutch sizes or to calculate fresh clutch weights. The clutch sizes of unparasitized nests (all but one of these was greater than four) suggest that virtually all females collected from these nests were experienced breeders (Aldrich and Raveling 1983). A t-test indicated that the calculated fresh weights of clutches from the post-laying sample (984.9 ± 165.8; N = 11) and the pre-hatch sample (1026.0 ± 111.2; N = 10) were similar (t = 0.7 two-tailed P = 0.509). Hence, differences in carcass composition of females in the two groups were presumably not the result of differences in either experience or the extent of body reserve use for clutch formation (based on calculated fresh clutch weights).

Table III-1. Number of incubating female Canada geese collected at two stages of incubation at two locations in 1985 and one location in 1986.[1]

		Post-laying		Pre-hatching	
Year	Area	Date	N	Date	N
1985	Rolling Hills Reservoir (RHR)	April 20	4	May 9	4
	Gleddie Lake (GL)	April 21,22	5	May 10	4
1986	Rolling Hills Reservoir (RHR)	April 11	5	May 2	4

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[1] Eggs were collected and artificially incubated to confirm and refine estimated day of incubation at the time of collection. Goslings hatched from these eggs were reared at the BWC until mid July and were then released by Alberta Fish and Wildlife.

Table III-2: Body weight and composition[1] (mean ± SD) of incubating female Canada geese at two stages of incubation.

	Stage of Incubation				
	Post-laying (N=13 or 14)[2]	Pre-hatching (N=12)	Difference	t value[3]	P
Body weight (g)	3817.5 ± 229.0	3186.1 ± 196.0	631.4 (17%)	7.4	<0.001
Fat content (g)	510.7 ± 127.3	65.6 ± 31.6	445.1 (87%)	12.6	<0.001
Protein content (g)	761.9 ± 49.1	714.0 ± 47.8	47.0 (6%)	2.4	0.024

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[1] Excluding water (which can be calculated by multiplying protein content by a factor of 1.89), feathers, grit, ingesta and skeleton.

[2] The neck of one specimen was completely severed during cervical dislocation. This caused considerable blood loss from this specimen. Hence body weight and protein weights of this specimen were excluded, but fat weight was used.

[3] Pooled t-test, one-tailed probability.

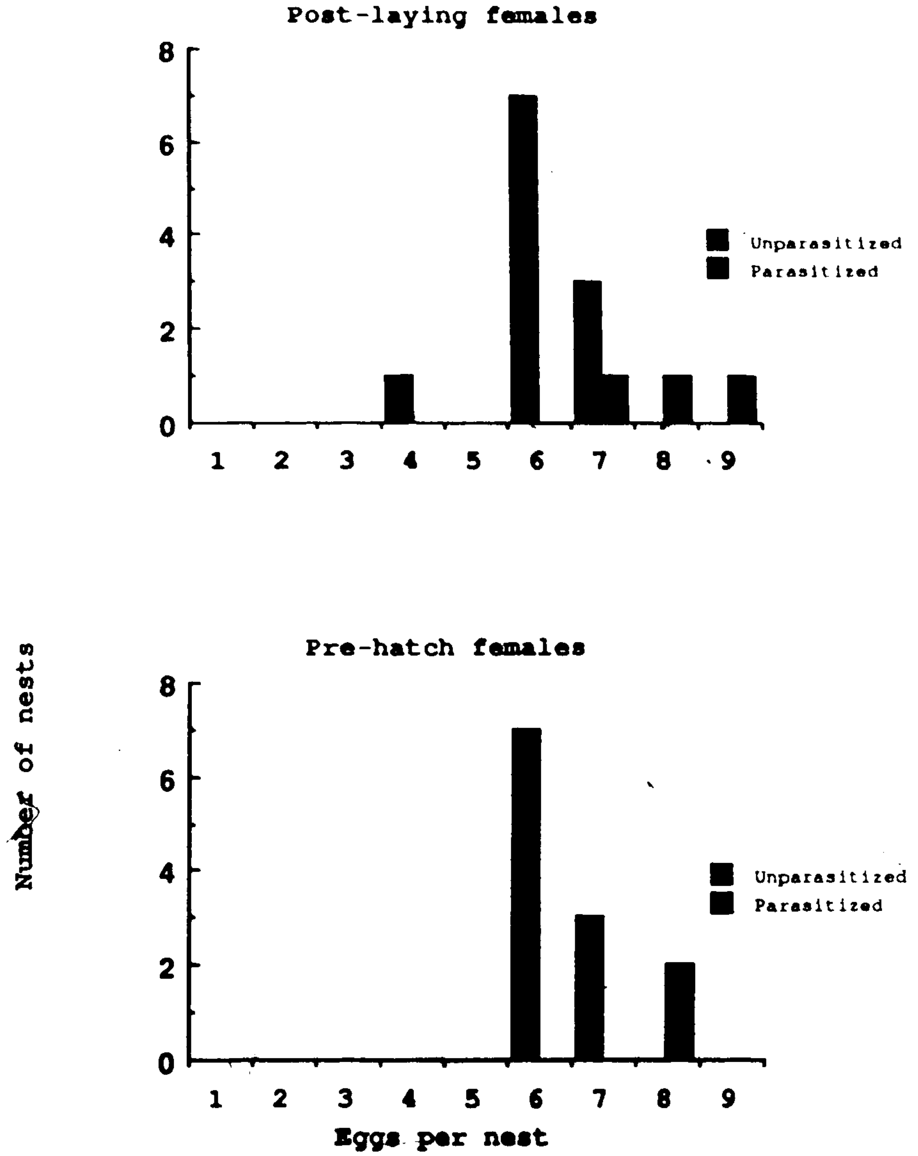

Fig. III-1: Numbers of presumed parasitized and unparasitized nests of female Canada geese taken at onset of incubation (post-laying) and at end of incubation (pre-hatch) based on egg size and shape and laying rate.

Ingesta Weight

The anterior portion (approximately the first third) of the small intestine never contained substantial amounts of ingesta. The absence of ingesta from this portion of the gut resulted presumably from more rapid passage of ingesta through the small intestine than through the ventriculus. With the exception of the anterior portion of the small intestine, I never observed an empty portion of gut (exclusive of the ceaca) seperating two portions that contained ingesta. This suggests that all ingesta in each goose had been collected on a single recess.

One pre-hatch female was collected approximately 95 min after she completed a recess during which she had fed rapidly for 13 min. This goose was observed on her nest for 66 min before she took the recess (total recess length = 20 min), and throughout the 95 min that separated her recess and her collection. When collected, this goose's esophagus still contained 1.9 g (dry weight) of vegetation. The anterior portion of the small intestine was empty, but the middle and posterior portions were full. This confirms that the absence of food from the anterior portion of the small intestine did not indicate that ingesta was collected on two separate recesses. The dry weight of all ingesta in this goose's gut was 20.2 g This rate of grazing (20.2 g in 13.0 min) is equivalent to 93.2 g dry weight per h or 1.6 g dry weight per min.

Most post-laying females were feeding very little or not at all; half contained < 2 g of ingesta, and only one contained > 8 g (Fig. III-2). This contrasts with the situation among pre-hatch females, all of which had some food in the gut. Ingesta weights from pre-hatch females varied considerably, being uniformly distributed between < 4 and > 22 g (Fig. III-2). Incubating Canada geese had significantly more (Mann-Whitney U = 151.5 P = 0.0002) ingesta in their guts just prior to hatch (N = 12; median = 10.3 g dry weight) than they did post-laying (N = 14; median = 1.9 g dry weight).

A trend toward an inverse relationship between ingesta weight and fat content of post-laying females (N = 14: Spearman rank.

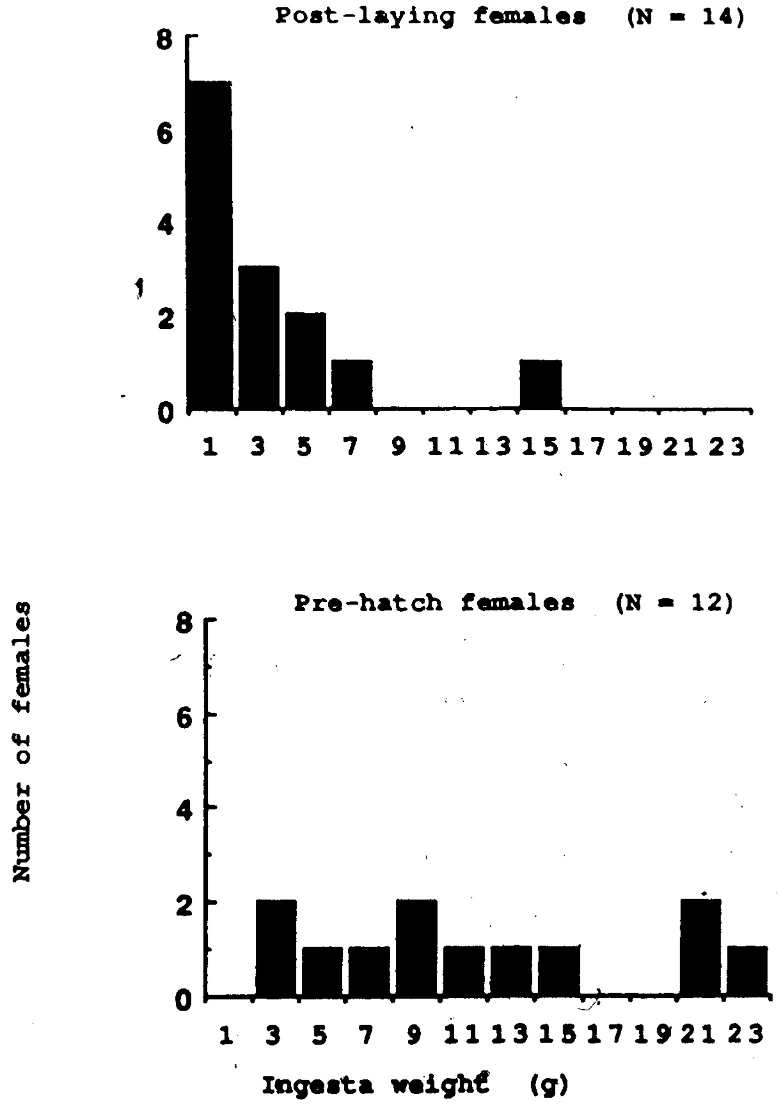

Fig. III-2: Frequency distribution of dry weights of ingesta from the guts of female Canada geese taken at onset (post-laying) and termination (pre-hatch) of incubation.

correlation coefficient = -0.438; P = 0.059) suggests that variation in ingesta weight was a function of the relative demand for exogenous energy (inversely related to fat reserves) and the female's willingness to feed, rather than the female's ability to obtain food. I conclude this because, if variation in ingesta weight reflected a female's ability to consume food, then I would have predicted a direct relationship between fat content and ingesta weight (assuming that a female's ability to consume food was reflected in higher fat content). Such was not the case.

The ability of one of the pre-hatching females to collect 20.2 g dry weight of food in only 13 min of feeding suggests that food was readily available at the time of the pre-hatch collection in at least some locations. Since incubating females sometimes fly to areas away from their insular nesting territories to feed (Ewaschuk 1970) all females should have had access to exploitable food sources. Hence, variation in ingesta weight among pre-hatching females also appears to be the result of differences in the demand for food rather than a female's ability to obtain it.

Six of the collected females had some ingesta in their esophagi. Esophageal contents were composed entirely of upland grasses. No sedge leaves or seeds were found. By far the most prevalent species was Sandberg's blue grass (*Poa sandbergii*). Traces of northern wheatgrass (*Agropyron dasystachum*) and blue grama grass (*Bouteloua gracilis*) were also identified.

Incubation Rhythms and Recess Behavior

The mean length of incubation recesses was similar for females incubating clutches of four and more than four eggs, but there was no overlap in the number of recesses taken by these groups (Table III-3). Females incubating clutches of five or more eggs (presumably experienced breeders) took at most two recesses per day. The two females that were incubating clutches of four eggs (presumably first time breeders) took at least three recesses per day.

Two females with clutches of five or more eggs that were

Table III-3: Incubation behavior during the final week of incubation of female Canada geese presumed to be either experienced or inexperienced breeders.

Clutch size[1]	Nest #	# Days observed	Recesses/day mean (range)	Recess length mean ± SD (N)	Attentiveness[2] mean (range)
Five or more eggs	1	2	1.0 (1-1)	27.5 ± 2.1 (2)	98.1 (98.0-98.2)
	2	3	1.7 (1-2)	26.4 ± 14.0 (5)	96.9 (94.4-99.1)
	3	1	1.0 (---)	22.0 ± ---- (1)	98.5 (----)
Four eggs	1	2	7.0 (4-10)	14.3 ± 7.8 (14)	93.0 (91.5-94.5)
	2	3	3.3 (3-4)	28.6 ± 18.0 (10)	93.4 (90.2-96.7)

[1] The first group was assumed to be experienced breeders (second-time or later breeders) and the second was assumed to be inexperienced breeders (first-time breeders).

[2] Attentiveness was calculated as the % of the 24-h period that females were thought to be on their nests. Since incubation behavior was not recorded after dark, I assumed that females only left their nests during the day.

observed for one entire recess on Days 18 and 24 of incubation spent 20 of 33 min (61%) and 14 of 16 min (88%) feeding. One female with a clutch of six eggs was observed for two complete recesses: on Day 15 of incubation, 12 of 19 min (63%) were spent feeding, and on Day 20, 13 of 20 min (65%) were spent feeding.

Energy from Body Reserves and Food Intake

Energy from fat catabolism supplied most (83%) of the energy requirements of incubating females (Table III-4). Energy derived from protein catabolism during incubation was minimal (4.2%). Based on the difference between the energy available from the catabolism of body reserves (between Day 3 and Day 24 of incubation) and the total energy requirement for that period, females presumed to have breeding experience should have obtained an average of 13% (100% - 87%; Table III-4) of their energy requirement from food over that period (Days 3 to 24).

The median contribution of exogenous energy derived from feeding during a single recess taken early in incubation (1.3% - Table III-4) was much less than this apparent average requirement. The median energy contribution attributable to food consumed on a single recess during the final week of incubation (7.2% - Table III-4) was 5.5 times as great as during early incubation, but was still considerably less than the calculated average requirement for exogenous energy (100% - 87% = 13%; Table III-4).

Since one to two recesses per day seemed to be typical of experienced breeders (Table III-3), it would seem that the median experienced female derived 1.3 to 2.6% and 7.2 to 14.4% (depending on the number of recesses per day) of its energy requirement from food in early and late incubation, respectively. Assuming that the change in the amount of food collected per recess occurred at a constant rate, then a female taking a single recess per day and consuming the median amount of food per recess would have acquired 4.3% ((1.3 + 7.2)/2) of her energy requirement from food between Day 3 and Day 24 of incubation. A female taking two recesses per day and consuming the median amount of food per recess would have

Table III-4: Energy required (kcal/d) by incubating female Canada geese and its availability from various sources.

Period of Incubation	Energy Required[a]	Source	Energy Provided	% of total Required
		<u>Body reserves</u>		
Days 3 - 24	230.5	Body Fat	190.8[b]	82.8
		Protein	9.6[c]	4.2
		Total	200.4[d]	87.0
		<u>Ingesta/recess</u>[e]		
Day 3	244.4	Minimum	0.0	0.0
		Median	3.1	1.3
		Maximum	25.7	10.5
Day 24	215.1	Minimum	4.3	2.0
		Median	15.4	7.2
		Maximum	40.2	18.7

[a] Based on the equation of Aschoff and Pohl (1970): BMR (kcal/d) = 73.5(ave. weight in kg)0.734 and Raveling's (1979) cost of incubation (1.25 x BMR).

[b] Based on the total decline in fat (g) between Days 3 and 24 divided by 21 and multiplied by the energy equivalent for fat (9.0 kcal/g): (445.1 g/21 d) x 9.0 kcal/g = 190.8 kcal/d.

[c] Based on the total decline in protein (g) between Days 3 and 24 divided by 21 and multiplied by the energy equivalent for protein (4.3 kcal/g): (47.0 g/21 d) x 4.3 kcal/g = 9.6 kcal/d.

[d] The sum of energy provided by endogenous fat and protein.

[e] Based on corrected (for absorption) ingesta weights, the energy content of spring grass (4.277 kcal/g) and the retention rate (digestibility) of that grass by geese (0.40; Owen 1980).

acquired 8.5% ((2.6 + 14.4)/2) of her energy requirement from food over that period.

Three or four recesses per day appeared to be typical of inexperienced breeders (Table III-3). Assuming that inexperienced breeders obtained the median amount of food per recess that was observed among females presumed to be experienced breeders, then inexperienced breeders would have derived 3.9 to 5.2% of their energy requirement from food in early incubation and 21.6 to 28.8% of their energy requirement from food during late incubation. However, since inexperienced females need to maximize exogenous energy acquisition (Aldrich and Raveling 1983), it may be more reasonable to assume that they consumed the maximum amount that was recorded in presumed experienced breeders. If the latter assumption is correct, inexperienced females would have derived 31.5 to 42.0% (3 to 4 X 10.5; Table III-4) and 56.1 to 74.8% (3 to 4 X 18.7; Table III-4) of their energy requirement from food during early and late incubation.

DISCUSSION

Ingesta Weight

The increase in dry weights of ingesta recorded in this study supports an earlier report of a similar phenomenon in incubating snow geese (Ankney 1977), and substantiates suggestions that Canada geese also increase their reliance on food intake as incubation progresses (Aldrich 1983, Bromley 1984).

I suggested that low ingesta weights, particularly early in incubation, reflect a decision not to feed rather than difficulty in obtaining food. Nevertheless, of the four recesses that I observed in their entirety, all contained at least 12 min of feeding (from 61-88% of total time off the nest). While I observed no recesses that involved no feeding; Cooper (1978) and Aldrich (1983) have each recorded recesses that contained little or no feeding. The fact that I did not observe recesses of this kind may reflect both the timing of my observations and a potential bias in my methods (in addition to the small number of recesses observed). All recesses observed in their entirety were recorded in the last half of the incubation period when females seemed to rely more heavily on food intake. Moreover, I observed several females until one of them left the nest and then followed the recess behavior of that female. Hence, my observations may have been biased towards females that left the nest more frequently than the rest of the population. As recess frequency and feeding activity are both inversely related to body reserves (Aldrich 1983) my observations may have been biased toward females that were inclined to spend a higher than average proportion of their recess time feeding.

Energy from Body Reserves and Food Intake

The use of body reserves during incubation has now been investigated in four subspecies of Canada geese (*B. c. minima, occidenatlis, moffitti, and maxima*). Females of *B. c. moffitti* derived more (87%) of their incubation energy requirement from body reserves than either of the smaller subspecies (Table III-5). This is consistent with the relationship reported by Thompson and Raveling (1987); larger geese derive more of their incubation energy requirement from body reserves than smaller geese. However, contrary to this trend, incubating *B. c. moffitti* also derive more of their energy requirement from body reserves than do the larger *B. c. maxima* (71.5%).

Since food supplies an increasing proportion of the total energy requirement as incubation progresses (Table III-4), some of this difference may result from the fact that my pre-hatch specimens were collected on approximately Day 24 of incubation while *B. c. maxima* females were collected on Day 26 (post-laying females were collected on approximately Day 3 of incubation in both studies). However, this difference could not explain very much of the difference between *B. c. moffitti* and *B. c. maxima*. Even if all *B. c. moffitti* females had taken two recesses per day and consumed the maximum amount of food recorded on each of Days 25 and 26 of incubation, their body reserves would have supplied an average of 85% ([(2 d x 63%) + (21 d x 87%)]/23 d) of their total energy

Table III-5: Calculated proportion of energy required during incubation that is supplied from body reserves in various subspecies of Canada geese (*Branta canadensis*).

Subspecies	Source	Post-laying body weight	% Energy from body reserves
B.c. minima	Raveling 1979	1390	48.0
B.c. occidentalis	Bromley 1984	3206	66.1
B.c. moffitti	this study	3792	87.0
B.c. maxima	Mainguy and Thomas (1985)	4162	71.5[a]

[a] My calculations

requirement over the 23 d period.

Differences in the abilities of geese to repel predators (or in the types of predators present) and in the level of energy reserves that females retain after laying may explain differences in the use of body reserves by different groups of geese during incubation (Thompson and Raveling 1987). However, I am unaware of any predator-related difference that could account for greater use of body reserves by *B. c. moffitti* than by *B. c. maxima*. Further, *B. c. maxima* retained more than twice as much fat on Day 26 of incubation (166 ± 18 g; Mainguy and Thomas 1985) as *B. c. moffitti* contained an average of 24 d after they began incubation (66 ± 32 g; Table III-2). Hence, the availability of body reserves does not appear to explain the difference in the proportion of the incubation energy requirement met by reserves.

Ewaschuk and Boag (1972) reported that harassment of incubating females during the absence of their ganders was a major cause of nest failure among densely nesting *B. c. moffitti* in southern Alberta. They suggested that the presence of sufficient food (especially on small territories) might be a factor affecting the presence or absence of the male. Since *B. c. moffitti* nest at higher densities in southern Alberta (18.4-24.7 nests/ha; Ewaschuk and Boag 1972) than the *B. c. maxima* in Toronto (0.5 nests/ha; Mainguy and Thomas 1985), there may be greater selection pressure for female *B. c. moffitti* to rely on body reserves so that they do not compete with their mates for food on the nesting territory.

Since inexperienced females appear to retain smaller energy reserves after laying than experienced females (Aldr[illegible] Raveling 1983), the inclusion of a higher proportio[illegible] inexperienced females in samples of *B. c. maxima* taken on Day 3 of incubation than in those of *B. c. moffitti* may also explain the greater apparent use of body reserves by *B. c. moffitti*.

Since experienced female *B. c. moffitti* derive an average of 87% of their energy requirement from body reserves between Day 3 and Day 24 of incubation, they must presumably derive an average of 13% of their energy requirement from exogenous food sources during that period. However, the average of the median proportions of energy supplied by food intake consumed on a single recess at Day 3 and at Day 24 was only 4.3% (1.3 + 7.2/2; Table III-4). Thus, the median experienced female would derive only 8.6% (4.3% x 2) of its energy requirement from food even if it took two recesses each day (assuming that the increase in the amount of food consumed per recess occurred at a constant rate). This is somewhat less than the average energy reserves of post-laying and pre-hatch females suggests (100 - 87 = 13%; Table III-4). Zadworny (1985) suggested that uric acid produced by incubating turkey (*Meleagris gallopavo*) hens was re-used by ceacal microorganisms, and that these microorganisms in turn supplied the hens with metabolizable substrates. If this occurs in incubating geese, it may explain the difference between the calculated demand for exogenous energy (based on changes in body composition) and energy provided by direct food intake (based on ingesta weights).

Owen (1980) reported that incubating snow geese (*Chen caerulescens caerulescens*) maintained their body weight during the final stages of incubation and suggested that they might be able to derive their entire energy requirement from food at this time. While it is conceivable that *B. c. moffitti* could meet their entire energy requirement from food intake in the last week of incubation it would require them to take at least six recesses per day, based on maximum food intake recorded per recess for birds collected in the final week of incubation. This recess frequency seemed to be rare, even among inexperienced breeders, suggesting that it is unusual for these geese to meet their entire energy requirement from food even in the final week of incubation. Bromley (1984) demonstrated that body weight of female *B. c. occidentalis* could increase despite declining energy reserves because of protein replenishment (and associated water retention) concurrent with fat depletion. This phenomenon provides an alternative explanation for the ability of snow geese to maintain their body weights in the final stages of incubation.

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IV. STRUCTURAL SIZE AND CONDITION OF INCUBATING CANADA GEESE

INTRODUCTION

The body weight of birds can be partitioned into a relatively fixed component, composed primarily of structural elements and tissues, and a variable component made up of fat, muscle, water, and other constituents in excess of structural requirements. The constituents of the variable component are referred to as reserves (Owen and Cook 1977) or body reserves (Ankney and MacInnes 1978, Raveling 1979, Bromley 1984 and others). Estimates of the levels of reserves are referred to as condition indices. These indices have been related to survival (Hepp et al. 1986) and reproduction (Ankney and MacInnes 1978, Pattenden 1988) in waterfowl.

Condition indices should reflect the importance of different reserves relative to each other (Evans and Smith 1975). Since energy is the main requirement of incubating Canada geese *(Branta canadensis)* and fat supplies far more of that requirement than does protein (Raveling 1979, Bromley 1984), I used fat reserves as my measure of condition. Since virtually all body fat can be catabolized for energy production (Korschgen 1977, Ankney and MacInnes 1978), I equated total body fat with fat reserves.

The most widely applied condition index, suitable for use on live specimens, involves the use of body weight. Body weight alone provides a good estimate of condition for species that are relatively homogeneous in body size (Bailey 1979, Johnson et al. 1985), but it is not an acceptable index for species that are variable in size (Iverson and Vohs 1982, Whyte and Bolen 1984, Johnson et al. 1985). Several investigators (eg. Bailey 1979, Chappell and Titman 1981, Iverson and Vohs 1982) have found that dividing (or scaling) body weight by external measurements improves markedly the correlation with total fat content. The basis for this improvement is thought to be a relationship between the external measurements and the structural or fixed component of body weight. However, this relationship is often untested (Wishart 1979).

Johnson et al. (1985) used multiple regression equations that incorporated log-transformed body weights and morphometric data to develop equations that predicted the fat content (log-transformed) of sandhill cranes (*Grus canadensis*) and greater white-fronted geese (*Anser albifrons*) on the basis of body weight and morphometric data. They suggested that equations of this kind were preferable to scaling because they permitted different coefficients for weight and morphometric data. This is presumed to be advantageous because body weight is an exponential function of linear measurements.

This study was part of a larger investigation that evaluated effects of diet and body reserve manipulations on reproductive output of female Canada geese (Chapters II). The objective of this particular part of the study was to develop meaningful, non-destructive indices that could be used to evaluate the condition of small samples of females at specific points in the reproductive cycle (Days 3 and 24 of incubation). I began by examining the relationship between a series of external measurements and internal skeletal size. Measurements that were related to skeletal size were used to scale body weight, and the resulting indices were compared with total fat content. Total fat content was also regressed on body weight and external measurements (all variables log-transformed) in an effort to develop predictive equations.

Methods

A total sample of 27 incubating female western Canada geese (*B. c. moffitti*) was collected in the area of Brooks, Alberta during 1985 and 1986 (see Chapter III for details). Fourteen of these females were collected 2-5 d after they began incubation, and are referred to as post-laying females. Twelve females were in the final week of incubation when they were collected, and are hereafter referred to as pre-hatch females. One additional female was collected in mid-incubation (Day 17). Measurements from this female were used to compare morphometric data to overall skeletal.

size, but were excluded from all other analyses.

Geese were weighed to the nearest 25 g, measured, sealed in plastic bags, and frozen within a few hours of collection. Culmen, head (from the tip of the nail on the bill to the posterior extremity of the head), and tarsus were measured with Vernier calipers to the nearest 1.0 mm. Flattened wing chord and total length of the bird (tip of bill to tip of longest retrix) were measured to the nearest 5 mm with a wing chord board and a meter stick, respectively. All measurements taken from paired appendages were made on the left side unless that appendage was damaged.

Later, birds were thawed and their remiges and retrices were removed. Birds were then skinned and dissected. Soft tissue was removed (see Chapter III) from the skeletons and recombined with the skin. This material (the bone-free carcass) was then sealed in an individually-marked plastic bag and immediately refrozen. The humerus, tibiotarsus, and sternum lengths of the skeletons were measured to the nearest 1.0 mm with a metal ruler. These skeletal measurements were log-transformed and submitted to a principal component analysis (PCA) to produce an index of overall skeletal size. The skeletons of the geese were later prepared by the staff of the Alberta Provincial Museum and Archives, and are deposited therein.

The bone-free carcasses were homogenized in a commercial meat grinder (Butcher Boy TCA 22 - 1.5 horsepower). Carcasses were passed through the grinder five times and the material was mixed thoroughly between grindings. Replicate 30 g samples of the homogenate were oven dried (56° C) to constant weight, and fat was extracted with petroleum ether in a Soxhlet apparatus. Protein content was calculated according to the equations of Campbell and Leatherland (1980). A water:nitrogen ratio of 18.1:1 (average of constants reported for snow geese, *Chen caerulescens caerulescens*, collected in the first and third weeks of incubation), and a protein:nitrogen ratio of 6.25:1 were used in these calculations. Carbohydrates were ignored since their biomass is negligible in birds (Ricklefs 1974).

Statistical Methods

All statistical procedures were performed with the SPSSx statistical package. Statistical comparisons were considered significant when $P < 0.05$. Means are reported ± standard deviations. P values associated with correlation coefficients refer to one-tailed tests.

RESULTS

Structural Size

The skeletal size factor (SSF) extracted from the three skeletal measurements of 27 female geese explained 59.8% (average of the coefficients of determination, r^2, for the three measurements) of the variation in these measurements. SSF was more closely correlated with the length of the tibiotarsus than with the other two skeletal measurements (Table IV-1). Total length, tarsus, and head length were significantly correlated with SSF, but culmen and wing chord were not (Table IV-1). Correlation coefficients for total length and tarsus explained 36% and 32% of the variation in SSF, but the coefficient for head length explained only 16% of variation in SSF. Stepwise regression entered total length and tarsus, but none of the other external measurements in a predictive equation for SSF. The resulting equation explained just over half of the variation in SSF ($r^2 = 0.502$ $P = 0.0003$)

Incubating females were 17% lighter prior to hatch than they were in the post-laying period (Table IV-2). This difference was primarily the result of decreased fat content, but a significant decrease in protein content also contributed to the decline in body weight. SSF explained a significant ($P = 0.014$) portion (43.4%) of the variation in the body weights of post-laying females, but it did not explain a significant ($P = 0.505$) portion of the variation in the body weights of pre-hatch females, suggesting that variation in the level of protein reserves may have been greater among pre-hatch females than among post-laying females. Otherwise, decreased variation in fat content (a nonstructural component) between the

Table IV 1: Pearson correlation coefficients relating a skeletal size factor (extracted by principal component analysis from three skeletal measurements of 27 adult female Canada geese) to the skeletal measurements used and several external measurements

Measurement type	Measurement	N	r	P
Skeletal	Tibiotarsus	27	0.866	<0.001
	Humerus	27	0.726	<0.001
	Sternum	27	0.704	<0.001
External	Total length	26	0.597	0.001
	Tarsus	27	0.567	0.001
	Head	27	0.405	0.018
	Culmen	27	0.230	0.124
	Wing chord	27	0.161	0.211

Table IV-2: Body weight and composition (mean ± SD) of incubating female Canada geese at two stages of incubation.

	Stage of Incubation				
	Post-laying (N=13 or 14)[1]	Pre-hatching (N=12)	Difference	t value[2]	P
Body weight (g)	3817.5 ± 229.0	3186.1 ± 196.0	631.4 (17%)	7.4	<0.001
Fat content (g)	510.7 ± 127.3	65.6 ± 31.6	445.1 (87%)	12.6	<0.001
Protein content (g)	761.9 ± 49.1	714.0 ± 47.8	47.0 (6%)	2.4	0.024

[1] The neck of one specimen was completely severed during cervical dislocation. This caused considerable blood loss from this specimen. Hence body weight and protein weights of this specimen were excluded, but fat weight was used.

[2] Pooled t-test, one-tailed probability.

two periods (note standard deviations - Table IV-2) should have strengthened the relationship between SSF and body weight between the two periods.

Fat Content

Body weight was significantly (P = 0.010) correlated with the fat content of post-laying females (Table IV-3). While it was not significantly related to the fat content of pre-hatch females (P = 0.89) a trend was indicated. The absence of a significant relationship among pre-hatch females may reflect increased variation in the protein reserves of the females, but it may also be a function of the reduced level of variation (in absolute terms; note standard deviations Table IV-2) in the fat content of pre-hatch females (Smith 1984).

Scaling body weight by external measurements that were related to structural size did not consistently improve the associations between fat content and body weight (Table IV-3). This result is not particularly surprising since individual measurements explained at most 36% of the variation in SSF. Scaling by total length and head length did improve the relationship between body weight and fat content in pre-hatch females, but it detracted from the relationship in post-laying females. Hence, the improvement that was observed in the pre-hatch group was probably fortuitous.

Log-transformed body weight explained 34.1% of the variation in the log-transformed fat content of post-laying females (P = 0.036), but did not explain a significant portion of the variation in log-transformed fat content of pre-hatching females (Table IV-4). Incorporation of single external measurements did not improve the predictive power of body weight in either group (Table IV-4). The two external measurements that stepwise regression procedures included in a predictive equation for SSF did not improve the predictive power of body weight among post-laying females (Table IV-4). While these measurements did increase the predictive power of body weight among pre-hatch females the resulting equation still was not significant.

Table IV-3: Pearson correlation coefficients relating weight based condition indices to the fat content of incubating Canada geese during early (post-laying) and late (pre-hatch) incubation.

	Post-laying (N = 13)		Pre-hatch (N = 12)	
Condition Index	r	P	r	P
Body weight (BW)	0.6327	0.010	0.4161	0.089
BW/Total length	0.5210	0.034	0.4947	0.051
BW/Tarsus length	0.5491	0.026	0.2050	0.261
BW/Head length	0.5660	0.022	0.4784	0.058

Table IV-4: Coefficients of determination (r^2) and P values of regression equations predicting the fat content of incubating Canada geese during early (post-laying) and late (pre-hatch) incubation.

Independent variable(s)	Post-laying (N = 12)		Pre-hatch (N = 12)	
	r^2	P	r^2	P
Body weight (BW)	0.341	0.036	0.218	0.126
BW and total length (TL)	0.362	0.106	0.332	0.163
BW and tarsus length (TS)	0.343	0.122	0.327	0.168
BW, TL, and TS[1]	0.363	0.235	0.558	0.075

[1] I used both total length and tarsus length in conjunction with body weight, since stepwise regression procedures included both measurements in a predictive equation for SSF.

DISCUSSION

Gauthier and Bédard (1985) found that scaling the body weights of adult female greater snow geese (*Chen caerulescens atlanticus*) by a variety of external measurements failed to improve the relationship between body weight and fat content. This study of adult female western Canada geese confirmed their results. In contrast with these findings, Johnson et al. (1985) reported that scaling the body weights of male and female greater white-fronted geese (*Anser albifrons*) by external measurements did improve the relationship between body weight and fat content.

Male white-fronted geese were larger than females. Hence the incorporation of males and females in the same sample probably increased the range of structural sizes and external measurements considered by Johnson et al. (1985). Since increasing the range of values considered increases correlation coefficients (Smith 1984), the relationships between external measurements and overall structural size were probably stronger in the sample of male and female geese considered by Johnson et al. (1985) than in the samples of only females investigated by Gauthier and Bédard (1985) and me.

Johnson et al. (1985) demonstrated that multiple regression equations incorporating log-transformed body weights and external measurements provided better indices of fat content than scaled body weights. However, equations of this kind were not effective for incubating female Canada geese. As with scaling, the failure of these procedures to produce significant predictive equations for fat content is attributed to the relatively low proportion of the variation in overall skeletal size that these measurements explained (Table IV-1).

Since body weight is related to the fat content of post-laying females (Table IV-3), it can be used to compare the condition of females in this group. However, since it explains only 34.1% of the variation in fat content it is important to recognize that comparisons based on body weights will not provide rigorous tests for differences in condition. Significant differences in the fat content (and by definition condition) of female Canada geese at the beginning of the incubation period may be obscured by extraneous variation in body weight. Since body weight is not significantly related to the fat content of female Canada geese during the final week of incubation, it should not be used to compare condition among individual females at this stage of the nesting cycle.

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V. Concluding Discussion

This study investigated the impact of spring diet on body weights and reproductive output of Canada geese nesting in captivity. Studies of wild females nesting in the surrounding area were used to relate the captive study to the wild situation and to assess the relationship between body weight and condition.

Body weight was related to the condition (defined as fat content) of wild females during early incubation, but was not significantly related to the condition of females at the end of the incubation period. Even during early incubation, body weight explained only 34% of the variation in fat content. The relationships between morphometric measurements and structural size were not strong enough to warrant the incorporation of these measurements in condition indices for incubating females. Scaling body weights by the morphometric measurements did not consistently improve the relationship with fat content, confirming the result that Gauthier and Bédard (1985) obtained for greater snow geese (*Chen caerulescens atlanticus*). Likewise, these measurements (log-transformed) did not significantly increase the predictive power of regression equations based on body weight.

Since the relationship between body weight and the condition of wild females was only moderate at best, I used changes in body weight (either between periods within a year or between years at the same stage of the nesting cycle) to assess the impacts of diet treatments on the captive geese. This removed variation that would otherwise have been introduced by differences in structural size among individuals.

Captive females with reduced body weights (by previous diet restriction) that received an ad libitum (ad lib.) supply of high energy foods recovered body weight rapidly and concurrently with rapid yolk deposition. Females grazing on new growth of wheatgrass were able to increase their body weights before, but not during rapid yolk deposition (defined in this study as the last week before clutch initiation). Since western Canada geese arrive on their breeding grounds approximately 3 wk before laying begins (Ewaschuk 1970) females may be able to augment their reserves considerably after arrival on the breeding grounds provided that a high quality food source is available there.

A reduction in food availability reduced the proportion of pairs that nested, but did not affect any of the following variables: quantity of food used, egg size or number, body weights of nesting geese, or nest attentiveness. Herbage diets, which were lower in digestible energy than the control diet, reduced all of the above characteristics, suggesting that the digestible energy content (perhaps mediated by the level of palatability reducing phenols) of the diet used by laying geese is critical for maximum reproductive output.

Geese normally compensate for the relatively low digestibility of their grass diet by consuming large quantities of food (Sibly 1981). However, this tactic was not employed by laying females. The food consumption of females using crested wheatgrass (*Agropyron cristatum*) declined during laying despite food abundance. Continued interest in food by laying females (55% of available time spent feeding) in this study and in other studies of nesting geese (Inglis 1977, Fox and Madsen 1981, Aldrich 1983 and others) suggests that the decrease in quantity of food consumed does not result from a lack of appetite (anorexia). Very selective foraging and low estimated dry matter intake (1.07 kg/wk) by laying females that were using wheatgrass of good quality suggested that they may have been attempting either to maximize the quality of food ingested or to minimize the quantity of deleterious plant constituents ingested.

Buchsbaum et al. (1986) reported that palatability reducing phenols in plants result in the production of secondary metabolites in the gut that can interfere with protein absorption. Perhaps these secondary metabolites have the potential to interfere with protein metabolism at other sites. If this is true, then protein metabolism associated with egg formation (especially albumin secretion which occurs very rapidly) may require laying females to reduce their food intake in order to minimize the levels of these secondary metabolites in their blood streams. These secondary metabolites might also interfere with enzymatic activity necessary to produce linoleic acid (which occurs in eggs at much higher concentrations than in grass; McLandress and Raveling 1981)

Females that began incubation with reduced body weights were able to significantly reduce their rate of weight loss during early incubation even when they were restricted to low energy diets that had not allowed them to realize their potential egg and clutch sizes, suggesting that the quality of food available during laying may be more important than the quality of food available during the incubation period.

Wild females, presumed to have breeding experience, produced heavier clutches and were more attentive to those clutches (Chapter III) than captive females grazing on an abundant supply of wheatgrass. Since higher nest attentiveness is associated with larger body reserves (Aldrich and Raveling 1983), this suggests that wild females were able to derive more energy from the wild food resource than captive females derived from the abundant supply of wheatgrass. Very young vegetation (both grass and sprouting annuals) available to wild geese may have been more digestible (or more palatable) than the wheatgrass. Alternatively, the guts of the wild geese may have been better adapted than those of captive birds. While wild females may have brought larger reserves to their breeding grounds than captive females brought to the wheatgrass treatment, wild females could only have maintained those reserves if they encountered a high quality food source on the breeding grounds between arrival and laying (a period of 3 wk; Ewaschuk 1970).

Two factors may have reduced the digestibility of the wheatgrass used by captive females. First, an unusually warm spring in the year of the grazing study (1986) advanced the development of the vegetation (wheatgrass). Since digestibility declines with increasing plant maturity (Van Soest 1969), the wheatgrass may not have been as digestible as the herbage used by wild females (that responded to the unusually warm spring by nesting both earlier than normal and earlier than captive birds). Second, the wheatgrass was intensively grazed by the geese before they began laying, thereby removing the most digestible portions of the growing grass. Hence, the digestibility of the wild food resource (which was presumably not exposed to such intensive grazing) may have been higher than that of the wheatgrass at the time that laying occurred in the wild.

While these factors may have reduced the quality (digestible energy and/or palatability) of the wheatgrass, samples indicated that the wheatgrass was still of good quality (Table II-8). Hence, the reductions in egg size and number, and nest attentiveness that were recorded in this situation suggest that female *B. c. moffitti* require herbage of extremely high quality (or perhaps very well adapted guts) during laying in order to realize their potential egg and clutch sizes, and to retain body reserves after laying that allow them to maintain high nest attentiveness.

Wild *B. c. moffitti* females, presumed to have breeding experience, derived 87% of their energy requirement from body reserves between Days 3 and 24 of incubation. Consistent with the trend toward increased reliance on body reserves with increased body size (Thompson and Raveling 1987), this was more than smaller subspecies *B. c. minima* (48%; Raveling 1979) and *B. c. occidentalis* (66%; Bromley 1984). In contrast with the trend noted by (Thompson and Raveling 1987), incubating *B. c. moffitti* also derived more of their energy requirement from body reserves than larger *B. c. maxima* (72% according to my calculations using data from Tables 2 and 7 of Mainguy and Thomas 1985). Intraspecific strife in conjunction with higher nesting densities among *B. c. moffitti* nesting in southern Alberta (18.4-24.7 nests/ha; Ewaschuk and Boag 1972) than among *B. c. maxima* nesting in Toronto (0.5 nests/ha; Mainguy and Thomas 1985) may explain greater use of body reserves by *B. c. moffitti* than by *B. c. maxima*. Ewaschuk and Boag (1972) reported that nest desertion was a major cause of nest failure among *B. c. moffitti*, and that the presence of the male on the nesting territory was crucial to nesting success. They suggested that the male's ability to meet his nutrient requirements from food on the nesting territory may have been an important factor governing his presence or absence. Perhaps this provides additional selection pressure for females to rely on body reserves, so that they do not compete with their mates for food on their territories.

Food use was negligible for most females during early incubation and was variable in the final week of incubation. Some females were still using very little food in the final week of incubation, apparently because their body reserves were still sufficient to meet virtually all of their nutrient demands. Other females, presumed to have breeding experience, may have derived up to 37% of their energy requirement from food in the final week of incubation, and females presumed not to have breeding experience may have derived up to 75% of their energy requirement from food at that time.

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Appendix I: Calculation of Dry Matter Intakes from Defecation Rates and Feces weights

Defecation rates were estimated by the hourly block method of Bédard and Gauthier (1986). This method combines defecation counts from different subjects until the accumulated observation period equals or exceeds 1 h. Hourly defecation rates and variances for those rates are calculated by the following equations:

$Y = K/T$ var of $Y = K/T^2$

Where Y = unbiased minimum variance estimate of hourly defecation rate
K = the number of defecations for a given block of time
T = the duration of the block (in h)

Average defecation rates are then calculated by the equation:

$$\text{ave } Y = \left([1/M] \times \sum_{N=1}^{N} \sqrt{Y} \right)^2$$

Where N is the number of hourly blocks

The number of hourly blocks (N) obtained and the results of these calculations are summarized below.

	Females	
	Pre-laying	Laying
N	6	6
ave Y	4.813	4.211
var. of ave Y	0.622	0.089

Mean weight (mean of means from seven collections of ten feces each) of feces collected during the period that most females were forming eggs (pre-laying and laying periods; April 18 to May 2) was 2.1 g (SD = 0.4 N = 7).

This mean feces weight (MFW) was then used in conjunction with defecation rates and average retention rate for geese grazing on spring growth of grass (0.4; Owen 1980) to estimate hourly dry matter intakes (HDMI) for active females according to the formula:

$$\text{HDMI} = \text{MFW} \times \text{ave } Y \times (1/(1-0.4))$$

Daily activity periods (DAP) were calculated by subtracting the time that females spent loafing and attending the nest from the diurnal period (a 15 h period was actually used since the geese became active slightly before sunrise and remained active for a short period after sunset). These calculations follow.

Pre-laying Period

DAP = 15 - (15 x [% time loafing + % time attending nest])

DAP = 15 - (15 x [22.1 + 0])

DAP = 15 - 3.315

DAP = 11.685

Pre-laying Period

DAP = 15 - (15 x [% time loafing + % time attending nest])

DAP = 15 - (15 x [18.8 + 12.0])

DAP = 15 - 4.62

DAP = 10.38

The previously calculated HDMI were then mutiplied by the DAP and days per week (7) to provide estimates of dry matter intake per week.

DM/wk = HDMI x DAP x 7

These estimates were 1.38, and 1.07 kg/wk for females during the pre-laying and laying periods respectively.

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