The Auk 109(3):511-521, 1992

PHYSIOLOGY OF PROLONGED FASTING IN GREATER SNOW GEESE (*CHEN CAERULESCENS ATLANTICA*)

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ABSTRACT.—Greater Snow Geese (*Chen caerulescens atlantica*) may face periods of complete food deprivation during incubation in the High Arctic. We studied the ability of these birds to withstand a prolonged fast. We measured rate of mass loss, patterns of carbohydrate, lipid and protein utilization, and changes in resting metabolic rate in 11 captive geese subjected to complete food deprivation. Geese lost 44% of their initial body mass during fasting periods that ranged from 19 to 42 days (mean 34 days). The rate of mass loss reflected the three phases commonly associated with the changing rates of lipid and protein catabolism in homeotherms. Phase I (11 days) was characterized by a decreasing rate of body-mass loss and a rapid increase in plasma β-hydroxybutyrate level, indicating body-lipid mobilization. During phase II (22 days), the rate of body-mass loss stabilized at a low level. Plasma concentration of β-hydroxybutyrate peaked in the first half of phase II and then decreased. Plasma uric-acid level, an index of protein catabolism, increased during the second half. Resting metabolic rate of fasting geese was reduced by 38% below the pre-fast value, more than predicted from body-mass decrease alone. Phase III (3 to 4 days) was characterized by an increase in the daily rate of mass loss. Plasma concentration of uric acid increased markedly, while β-hydroxybutyrate values remained low and stable. Glycemia and total plasma protein level also started to fall. Greater Snow Geese did not tolerate fasting as long as larger birds, like penguins, probably because they were less efficient in sparing their protein reserves during phase II. Greater Snow Geese endurance of fasting may be limited by their use of flight, which ultimately limits their capacity to carry the large fat reserves required for prolonged fasting. *Received 30 April 1991, accepted 13 January 1992.*

IN WILD BIRDS, fluctuations in food availability may impose fasting for more or less predictable periods of time. Energy requirements of small passerines allow them to tolerate fasting in winter for only 10 to 37 h before dying (Kendeigh 1945, Ketterson and King 1977), but large birds of prey may be deprived of food for 11 to 13 days and remain in good health (Hatch 1970, Garcia-Rodriguez et al. 1987). Even in the presence of food, some species may fast because feeding conflicts with other important activities. Red Jungle Fowl (*Gallus gallus*; Mrosovsky and Sherry 1980), most penguins and petrels (Croxall 1982, Cherel et al. 1988b), and many Arctic- and temperate-nesting anatids (Korschgen 1977, Krapu 1981, Mainguy and Thomas 1985, Thompson and Raveling 1987, Ankney and Afton 1988, Parker and Holm 1980) greatly reduce their food consumption during egg laying and incubation. In these birds, only one parent incubates and it is not fed by its mate. Fasting endurance may have an adaptive value and be a key determinant of reproductive success in species facing a negative energy balance during nesting.

The reproductive success of nesting geese depends largely on the quality of nest attendance by females during incubation (Murphy and Boag 1989). To reduce risks of predation and intraspecific nest parasitism, females stay on the eggs and feed little from laying to hatching (Ryder 1970, Ankney and MacInnes 1978, Raveling 1979, Aldrich and Raveling 1983, Prop et al. 1984, Mainguy and Thomas 1985, Thompson and Raveling 1987). Males do not incubate, but assume most of the territorial defense and also reduce their food intake (Inglis 1977, Stroud 1982). They lose weight, though to a much lesser extent than females (Ryder 1975, Ankney 1977, Owen and Wells 1979).

In Lesser Snow Geese (*Chen caerulescens caerulescens*), females feed very little after completing laying. Without sufficient energy reserves to endure a long fast, some females do not complete incubation and may even die before its termination (Harvey 1971, Ankney and MacInnes 1978). Greater Snow Geese (*Chen caerulescens atlantica*) presumably also become anorexic during their 24-day incubation period (Lemieux 1959), although their nesting behavior is largely unknown.

Despite the obvious importance of fasting in

the life history of many species of birds, little is known about the behavioral and metabolic adaptations to food deprivation. This contrasts with the large number of studies dealing with foraging or feeding ecology. In the family Anatidae, physiological responses to long-term fasting have been studied only in Common Eiders (*Somateria mollissima*; Korschgen 1977) and domestic geese (*Anser anser*; Benedict and Lee 1937, Le Maho et al. 1981, Robin et al. 1987). Le Maho et al. (1981) and Robin et al. (1987) have described three phases associated with changes in the relative rate of mass loss, and the nature and quantity of fuels oxidized in fasting geese. These three phases have also been recognized in at least one other group of birds, the penguins (Cherel et al. 1987, 1988a, c, Robin et al. 1988), and in mammals such as rats (Goodman et al. 1980, Lowell et al. 1986).

In fasting domestic geese, phase I is short (3 to 8 days) and appears as an "adaptation" period, where proteolysis is progressively reduced while fat mobilization increases (Le Maho et al. 1981). During this period, daily rate of mass loss and resting metabolic rate also decrease progressively. Phase II is the longest period (23 to 35 days), during which rates of mass loss and metabolism remain low and fat becomes the main fuel. This permits the conservation of body proteins, which have not only caloric properties, but also vital structural and regulatory roles (Griminger and Scanes 1986, Owen 1989). Whereas phase II can be called an "economy" phase, phase III (up to 10 days), where body proteins are no longer spared and the daily rate of mass loss increases, corresponds to a "critical" period, although these physiological changes can be reversed.

Changes in certain blood metabolites are indicative of the type of energy reserves used during the three phases described for prolonged fasting. Plasma uric-acid concentration is an index of protein catabolism, because birds excrete mostly uric acid as an end product of metabolized nitrogen (Griminger and Scanes 1986). Also, β-hydroxybutyrate (β-OHB) is one of the ketone bodies produced after partial oxidation of the fatty acids resulting from triglyceride hydrolysis. In birds, plasma levels of β-OHB are subjected to greater variation than those of acetoacetate, and are related to lipid catabolism (Le Maho et al. 1981, Cherel et al. 1988b). Total plasma-protein concentration reflects the balance of circulating proteins, their release by muscle tissues, their synthesis by the liver, and their degradation.

The aims of our study were to investigate the ability of Greater Snow Geese to withstand a prolonged fasting period and to determine their patterns of carbohydrate, lipid and protein utilization in relation to the duration of the fast. Based on previous work on fasting birds (summarized in Le Maho 1983), we hypothesized that fasting geese should be able to: (1) maintain their glycemia and blood proteins; (2) minimize their use of body proteins; (3) increase their use of fat reserves; and (4) reduce their metabolic rate. To test these hypotheses, we measured changes in body mass, resting metabolic rate, and blood composition in geese fasting under controlled conditions.

METHODS

Study animals.—Sixteen adult geese, eight of each sex, were captured during spring migration along the St. Lawrence River estuary (Québec, Canada) in 1987 and 1988. Fasting experiments were conducted from 18 September to 21 November 1989, when birds were not molting, to eliminate changes in blood metabolites related to feather production (Mori and George 1978, Cherel et al. 1988a). During experiments, the birds were housed in individual cages (1 m^3) under a 12 L/12 D cycle at 20 to 24°C. Experiments on captive Greater Snow Geese were approved by the local Animal Protection Committee, which follows the guidelines issued by the Canadian Council of Animal Protection. Handling of geese was reduced to a minimum and performed only by trained staff to minimize stress.

Geese were acclimated to cages and manipulations during a pre-fast period of 36 days. During the last 10 days of this period, body mass, total lipid, resting metabolic rate, and hematologic variables were measured, and their average values were used as reference values for fed geese. Afterwards, 11 geese (6 males and 5 females) were deprived of food, while the remaining 5 birds served as a control group. Fatter geese were chosen as fasting subjects because prelaying Lesser Snow Geese typically have large endogenous reserves (Ankney and MacInnes 1978). Before and after the fast, geese were fed *ad libitum* with a commercial fowl mash (containing a minimum of 20% protein and 2.5% fat; Ralston Purina Canada, Inc.) and oat grain, and they received vitamin supplements. Water was provided at all times.

The fast was stopped two to four days after the birds reached phase III of long-term food deprivation (Le Maho et al. 1981, Robin et al. 1987, Cherel et al. 1988b). This stage was reached after 19 to 42 days of fast depending on individual birds (see results). However, three geese were fed just at the end of phase II

to ensure their well-being. One of these was showing signs of hypotensive episodes, as observed during long-term starvation in humans (Gries et al. 1977). The first bird to enter the critical phase died six days later, although refeeding had been attempted. One more goose died even though it had been successfully refed three days after entering phase III. This bird was found to have liver necrosis, which has also been noted in humans after a protracted fast (Cravario et al. 1975). These two geese were autopsied and their fat and protein content was determined following the methods of Gauthier et al. (1984a, b).

Blood sampling and body-mass measurement.—To avoid the high risks of anesthesia during implantation of catheters (Goelz et al. 1990), as well as possible injuries during catheter removal by the goose, blood was sampled by venous punctures. The tarsal and jugular veins were less subjected to hemorrhage or hematoma than wing vessels. Blood (3–5 ml) was collected in heparinized syringes, between 0900 and 1100, and stored immediately at 0 to 4°C. During the pre-fast period, blood samples were obtained at three-day intervals. During the fast, they were taken every morning for the first five days, when hematological changes were expected to be most rapid, and every second or third day thereafter. Blood samples were also taken each week in the five control-fed birds.

Geese were weighed at each blood sampling with a platform balance (accuracy ± 5 g). Total fat reserves were estimated prior to fasting, using the condition index described by Gauthier and Bédard (1985).

Blood analysis.—For assays of plasma protein and uric acid, plasma was obtained by centrifugation of blood samples at 1,000 × *g* during 20 to 25 min at 4°C. For β-hydroxybutyrate determination, blood was deproteinized with an equivalent volume of ice-cold perchloric acid 10% W/V before centrifugation. The supernatant was neutralized with potassium hydroxide 20% W/V and centrifuged. All plasma samples were stored at −15°C until the assays. Hematocrit was obtained by centrifugation (10 min, 14,000 × *g*) in standard microtubes.

Plasma concentrations of uric acid (Scheibe et al. 1974) and β-hydroxybutyrate (Williamson and Mellanby 1974) were determined using enzymatic reactions with reagents from Sigma Co. Total plasma proteins were assayed colorimetrically using bicinchoninic acid (Smith et al. 1985). Reagents and protein standards were from Pierce Co. Glycemia was measured in whole-blood droplets with a portable glucometer (Ames Glucometer II, Miles Co.).

Metabolic-rate determination.—We measured resting metabolic rates in 10 geese (5 of each sex). During the pre-fast period, the birds were unfed for 18 h prior to measurements, enough time to obtain the postabsorptive state (Benedict and Lee 1937, Smith and Prince 1973). During phase II of prolonged fasting, after 15 to 21 days of total food deprivation, metabolic rates were measured again on the same individuals. To accustom the goose to the experimental apparatus, the bird was placed in the metabolic chamber at least 2 h before the start of the experiment. The metabolic chamber volume was 73 L, allowing the bird to lie down or stand up, and find a comfortable position. It was built of Plexiglas and painted flat black inside. Air temperature (22–25°C) and gas composition in the chamber were homogenized by a small fan. Air was drawn through the cage at a mean flow rate of 6.1 L/min (at STP).

The rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) were measured in an open-circuit system. The air was desiccated with Drierite before passing through a paramagnetic O_2 analyzer (model E2; Beckman Instruments) and an infrared CO_2 analyzer (model IR-215; Beckman Instruments). Readings were made every 5 min over a period of 125 min (range 70–180 min). Analyzers were calibrated before and after each experiment with standard gases and pure nitrogen. The $\dot{V}O_2$ was calculated according to Tucker (1968) for measurements made during the most stable consecutive 25 min, usually toward the end of the experiment.

Data analysis.—To determine the length of the three fasting phases, linear regressions of daily rate of mass loss on time were fitted for each phase (Fig. 1). The transition point between each phase was defined as the point that maximized *R*-square values of regression lines on either side. Moreover, transition between phases II and III was easily recognized by a change of the slope from negative to positive. Results in a number of the figures are scaled to a period (35 days) representative of the average length of fasting. This facilitates the interpretation of changes in hematological variables as the length of fast varied among individual geese (see results).

A Wilcoxon matched-pairs signed-rank test was used when comparing the same individuals at different stages of the fast, while a Mann-Whitney *U*-test was used when comparing fasting geese with the control (fed) group. The Kendall's coefficient was used to test rank correlations and the relation between two variables (Sokal and Rohlf 1981). The means are presented with the corresponding standard error of the mean (SE). Significance level (*P*) was 0.05 for all statistical tests.

Results

No statistical differences were found between males and females for any of the measured variables. Therefore, data for the two sexes were pooled.

Duration of fast and body-mass loss.—Initial body mass and total fat reserves of the 11 fasted geese averaged 2.88 ± 0.06 kg (range 2.49–3.18 kg) and 20.3 ± 0.9% of the body mass (range 17.6–26.5%), respectively. These values are similar to

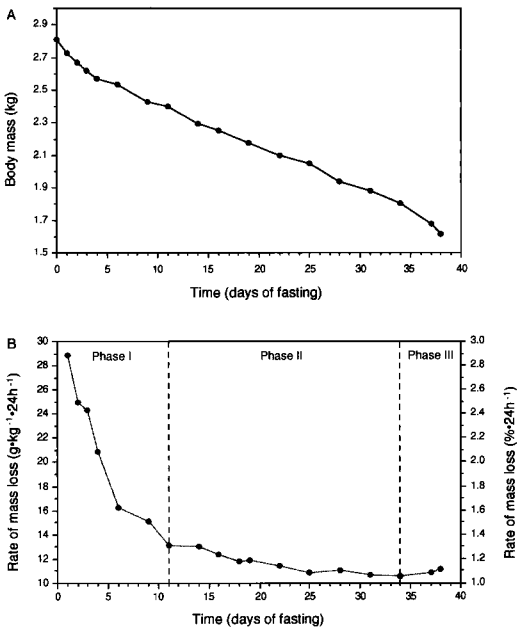

Fig. 1. Changes in (A) body mass and (B) rate of mass loss (relative to the initial body mass) in a fasting Greater Snow Goose.

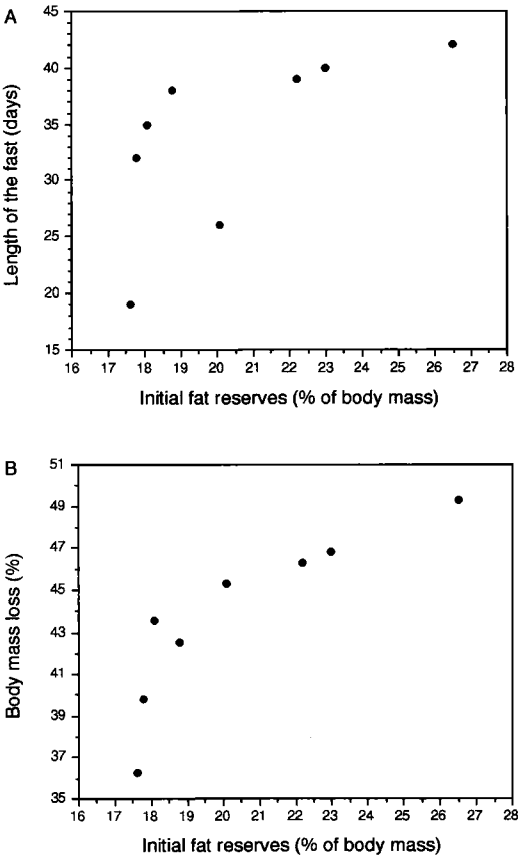

Fig. 2. Relationships between (A) the length of the fast ($T = 0.79$, $P < 0.01$) and (B) the body-mass loss ($T = 0.93$, $P < 0.01$) vs. initial fat reserves in Greater Snow Geese.

those found in Greater Snow Geese leaving the St. Lawrence River after the spring migration halt (Gauthier et al. 1984b). Body mass and total fat reserves in the five control geese averaged 2.54 ± 0.03 kg and 16.8 ± 0.6%, respectively, and these values did not change throughout the five-week experimental period ($P = 0.38$).

Phase I of the fast lasted 11 ± 1 days in Greater Snow Geese and was marked by a sharp decrease in the daily rate of mass loss from 25.0 ± 1.5 g/kg for the first day of fasting to 15.1 ± 2.4 g/kg at the end of phase I ($P < 0.001$; Fig. 1). During phase II, which lasted 22 ± 3 days, there was a further reduction to 12.8 ± 1.1 g/kg ($P < 0.01$). The phase III was characterized by a small increase in the daily rate of mass loss to 13.5 ± 1.1 g/kg on the last day ($P < 0.01$). The critical body mass, where the daily rate of mass loss starts to rise (the transition between phases II and III; Le Maho et al. 1976) was similar for all birds at 1.77 ± 0.05 kg (range 1.59–2.02 kg).

At the end of phase II, fasted geese had lost 37.6 ± 1.7% of their initial body mass. The eight geese that completed the experimental fasting period (i.e. those that reached phase III) fasted during 34 ± 3 days (range 19–42 days) and weighed 1.60 ± 0.06 kg at the end of phase III, a decrease of about 44% from their original body mass (range 36.3–49.3%). The length of the entire fast and the percentage of total mass loss were highly correlated with the initial fat reserve of the birds ($T = 0.79$ and $T = 0.93$, respectively, $P < 0.01$, $n = 8$; Fig. 2), but not to their initial body mass ($T = 0.29$, $P = 0.32$, and $T = 0.49$, $P = 0.62$, respectively, $n = 8$). Geese remained vigorous throughout phases I and II, standing up in alert position (head up), moving in their cages, and trying to bite during manipulations.

During the first two weeks of refeeding, geese ate 2.3 times as much food as before the fast (0.312 ± 0.011 kg vs. 0.136 ± 0.006 kg of mash per day). They gained weight rapidly (mean 65 g/day) and had recovered 35% of their mass loss after one week and 58% after two weeks.

Carcass composition.—The two fasted geese that

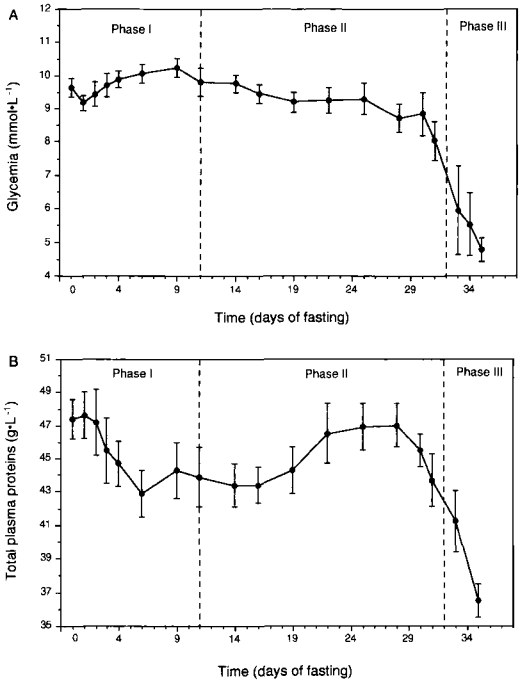

Fig. 3. (A) Glycemia level and (B) total concentration of plasma proteins during long-term fasting in Greater Snow Geese ($\bar{x} \pm$ SE; $n = 11$ for phases I and II, $n = 8$ for phase III).

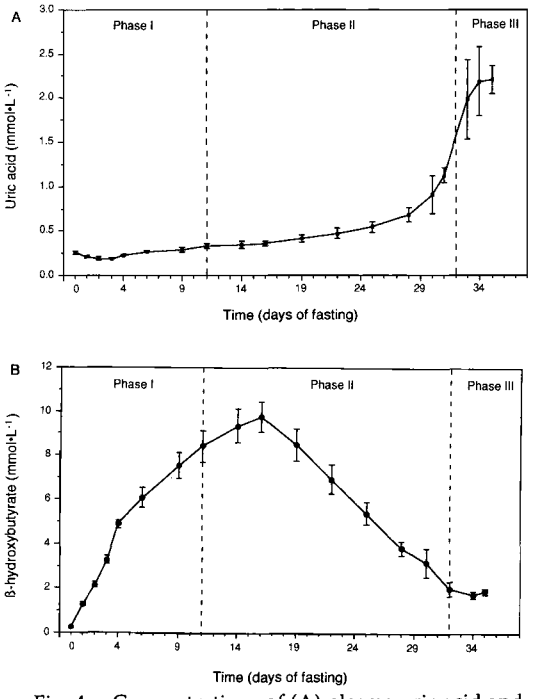

Fig. 4. Concentrations of (A) plasma uric acid and (B) β-hydroxybutyrate during long-term fasting in Greater Snow Geese ($\bar{x} \pm$ SE; $n = 11$ for phases I and II, $n = 8$ for phase III).

reached phase III, but died upon refeeding, depleted nearly all fat stores as only 11.0 ± 0.4 g (<1% of a body mass of 1.46 ± 0.07 kg) of lipids remained. Total body proteins also were considerably reduced to 293 ± 18 g (20.4% of body mass) compared to wild geese during spring staging (570 g; Gauthier et al. 1984a, unpubl. data).

Blood analysis.—The initial blood composition of fasted birds was not different from control birds ($P > 0.05$, $n = 11$ and 5; Mann-Whitney U-test). Blood composition of the control group did not change significantly ($P > 0.05$, $n = 5$; Kruskal-Wallis test) during the five-week experimental period.

Pre-fast glycemia (day 0; Fig. 3A) was 9.64 ± 0.27 mmol/L. Despite a nonsignificant decrease ($P = 0.21$) of blood glucose to 9.17 ± 0.22 mmol/L in the first day of fasting, glycemia was maintained around 9.5 mmol/L (range 8–11 mmol/L) throughout phase I and during almost all of phase II. From the end of phase II until the end of phase III, glycemia diminished rapidly to about one-half of the normal value (4.69 ± 0.32 mmol/L) on the last day of fasting ($P < 0.01$).

Pre-fast plasma protein concentration of fasted birds was 47.4 ± 0.12 g/L (day 0; Fig. 3B). Plasma proteins decreased to 43.1 ± 0.12 g/L ($P < 0.01$) midway in phase I of fasted birds. During the second part of phase II, they increased to levels near those found before food deprivation (mean 46.8 ± 0.16 g/L). Plasma proteins then decreased until the end of the experiment to 35.7 ± 0.06 g/L ($P < 0.01$) or 75% of the pre-fast value.

Geese had a plasma uric-acid level of 0.26 ± 0.02 mmol/L before fasting. In contrast to glucose and protein levels, the plasma concentration of uric acid increased considerably during the fast (Fig. 4A), after a slight but significant decrease ($P < 0.001$) to 0.189 ± 0.016 mmol/L during the first 48 h of fasting. From day 2 to the later part of phase II, uricacidemia increased slowly to 0.54 ± 0.06 mmol/L ($P < 0.001$). Thereafter, it rose very rapidly until the last day of phase III, to 2.32 ± 0.16 mmol/L ($P < 0.01$), more than eight times the normal value.

The plasma level of β-hydroxybutyrate (β-OHB) was 0.25 ± 0.04 mmol/L before the fast (Fig. 4B). After only one day of complete food

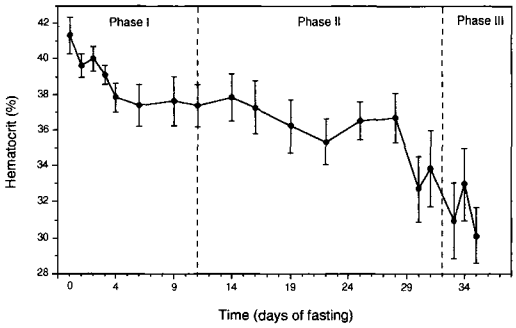

Fig. 5. Hematocrit level during long-term fasting in Greater Snow Geese ($\bar{x} \pm$ SE; $n = 11$ for phases I and II, $n = 8$ for phase III).

deprivation, β-OHB level had increased 4.6 times ($P < 0.001$) to 1.30 ± 0.10 mmol/L. It reached a maximum of 41 times the normal value at the beginning of phase II (10.2 ± 0.6 mmol/L), then declined to 2.04 ± 0.19 mmol/L at the beginning of phase III, and remained at this value, which is still far above the level observed in birds that were fed.

The hematocrit was 41 ± 1% before the fast. It decreased significantly to 38.1 ± 0.8% ($P < 0.05$) during the first four days of phase I (Fig. 5). Thereafter, it fluctuated slightly around 37.0 ± 1.5% until the end of phase II, and finally dropped to 30.8 ± 1.2% ($P < 0.01$) during phase III. Positive correlations were observed between hematocrit and total plasma proteins ($T = 0.42$, $P < 0.05$, $n = 8$), and between hematocrit and glycemia ($T = 0.50$, $P < 0.01$, $n = 8$).

Resting metabolic rate.—The resting metabolic rates (*RMR*) of 10 geese in pre-fast period averaged 7.76 W (Table 1; range 6.73–9.71 W), a value close to the predicted one (8.2 W) for a 2.93-kg nonpasserine bird (Lasiewski and Dawson 1967). Fasting significantly reduced ($P < 0.001$) *RMR* by 38 ± 4% to 4.77 W (range 4.06–5.90 W), as shown by measurements taken during phase II of the fast. The mass-specific *RMR* also dropped significantly ($P < 0.01$), from 2.7 to 2.2 W/kg, whereas allometric equations would have predicted birds of a lower mass to have a higher mass-specific *RMR* of 3.3 W/kg (Lasiewski and Dawson 1967).

Respiratory quotients (*RQ*) measured before the fast and during phase II were similar, averaging 0.71 ($P = 0.48$; Table 1). This low value was expected, because birds obtain their energy mainly from fat and protein reserves either in the postabsorptive state (Robbins 1983) or during phase II of the fast. Uric acid of bird excreta contains more oxygen and less nitrogen than urea excreted by mammals. This results in a *RQ* value for protein catabolism in birds closer to that for lipid catabolism.

DISCUSSION

This study demonstrates that Greater Snow Geese can endure a fast several days longer than their incubation period (34 vs. 24 days, respectively) providing they enter the fasting period with sufficient fat reserves (≥20% of body mass). It also shows that changes in body mass, utilization of energy reserves, and resting metabolic rate in fasting Greater Snow Geese follow the typical three-phase pattern described for homeotherms. Variations in body-mass loss result from changes in the composition of the tissues catabolized and in energy expenditure. This pattern is characterized by a preferential mobilization of lipids, which are the most efficient and abundant form of energy storage, during the longest period of the fast.

Phase I.—The rate of body-mass loss is very rapid during the first 24 to 48 h of the fast. In humans, this phenomenon has been attributed mostly to a major salt and water diuresis (Van Itallie and Yang 1977, Felig 1979, Owen 1989). In domestic geese (Le Maho et al. 1981), and presumably in Greater Snow Geese, dehydra-

TABLE 1. Resting metabolic rates (*RMR*) before fasting and during phase II of fasting in Greater Snow Geese ($\bar{x} \pm$ SE, $n = 10$).

	Before	During
RMR (W)	7.76 ± 0.31	4.77 ± 0.22*
Observed specific *RMR* (W/kg)	2.66 ± 0.10	2.21 ± 0.07*
Observed *RMR*/Predicted *RMR*[a]	0.94 ± 0.04	0.72 ± 0.02*
Respiratory quotient (*RQ*)	0.72 ± 0.01	0.71 ± 0.01
Body mass (kg)	2.93 ± 0.07	2.16 ± 0.05*

* $P < 0.01$.

[a] Lasiewski and Dawson's equation (1967).

tion is not significant. The high loss of body mass during the first 24 h of fasting (70 ± 6 g) may be caused by the emptying of the alimentary tract and a high catabolic rate of endogenous reserves.

The progressive reduction in the rate of body-mass loss during phase I may be attributed to a shift in the metabolic fuel from protein and glycogen to lipid, as well as to a reduction in metabolic rate. Protein and glycogen have lower caloric values (18.0 and 17.6 kJ/g, respectively) than lipids (39.3 kJ/g; Pond 1981), and oxidation of the former requires concomitant elimination of their solvent and/or hydration water. The decrease in specific *RMR* probably occurs during phase I in Greater Snow Geese, as has been observed in domestic geese (Le Maho et al. 1981) and in King Penguins (*Aptenodytes patagonica;* Le Maho 1983). Additional decreases in *RMR* during phases II and III are nearly in proportion to the actual body mass of the bird (Le Maho 1983, Cherel et al. 1988b). Similar reduction of basal metabolic rate during protracted fasting has been described in birds and mammals, including humans (Shapiro and Weathers 1981, Le Maho 1983, Chwalibog and Thorbek 1989, Owen 1989).

The changes in plasma uric acid, β-OHB and total proteins observed in Greater Snow Geese also indicate a shift in use of protein versus lipid in phase I. The decrease in plasma proteins presumably followed a reduction in blood concentrations of several glucogenic amino acids, such as alanine, serine, glutamine, lysine and others, as reported for mammals and birds during the first days of fasting (Cuendet et al. 1975, Brady et al. 1977, 1978, Freminet and Leclerc 1980, Goodman et al. 1980, Le Ninan et al. 1988).

Maintenance of glycemia is critical for homeotherms, because many tissues and cells depend upon blood glucose (i.e. central nervous system, erythrocytes, leukocytes, renal medulla, etc.; Cahill 1970, Moon 1988). Blood glucose concentrations in birds are twice those in mammals, and these levels are maintained throughout fasting (Langslow 1978, Hazelwood 1986). This was also the case during phase I and almost all of phase II of the fast in Greater Snow Geese. The slight decrease that appeared after 24 h of food deprivation may be associated with a depletion of glycogen reserves (Hazelwood 1986), as hepatic and muscular glycogens represent less than 1% of the total pre-fasting energy reserves in homeotherms (Cahill 1970, Cherel et al. 1988b). Thereafter, several physiological mechanisms, not entirely understood (Groscolas 1986, Boyle et al. 1989), are responsible for the prevention of hypoglycemia. Among them is an increased rate of gluconeogenesis (Groscolas and Rodriguez 1981, Moon 1988, Owen 1989) coupled to protein and triglyceride catabolism, taking place mainly from lactate, glycerol, pyruvate and alanine substrates in birds (Langslow 1978). The often observed decrease in glucose turnover rate (Brady et al. 1977, Streja et al. 1977, Freminet and Leclerc 1980, Groscolas and Rodriguez 1981, Riesenfeld et al. 1981) can be linked to a progressive reduction of glucose utilization by tissues that can oxidize other substrates such as fatty acids or ketone bodies (Felig 1979, Owen et al. 1983, Owen 1989). During long-term fasting, ketone bodies can be oxidized by the brain as a substitute for glucose, and the rate of consumption is concentration dependent (Robinson and Williamson 1980, Owen 1989). After a few days of food deprivation, ketone-body utilization by tissues can contribute to 30 to 40% of the total caloric requirements in humans (Owen et al. 1983) and can indirectly spare protein reserves by reducing gluconeogenesis (Felig 1979, Robinson and Williamson 1980, Anonymous 1989).

Phases II and III.—In phase II, the rate of body-mass loss was markedly reduced and maintained at a low and slightly decreasing level. This slow loss of mass was associated with low concentrations of plasma uric acid and ketosis. Such a pattern is characteristic of fasting animals, including humans, which are sparing body proteins and preferentially oxidizing lipids (Brady et al. 1977, Goodman et al. 1984, Cherel et al. 1987, Robin et al. 1988, Owen 1989). However, half-way through phase II until the end of the fast, opposite changes in plasma β-OHB and uric acid indicate that lean tissue catabolism had begun to increase while fat mobilization was decreasing. A similar augmentation of proteolysis also occurred before phase III in domestic geese (Le Maho et al. 1981, Robin et al. 1987). In contrast, high ketone-body levels, and probably their protein-sparing effects, were maintained during all of phase II in penguins (Cherel and Le Maho 1985, Cherel et al. 1987). The greater variation in plasma β-OHB and uric-acid concentrations of geese compared to penguins during this phase (Cherel and Le Maho 1985, Cherel et al. 1987, Robin et al. 1988) suggests that replacement of lipids by proteins as the

principal energy source in geese is more progressive than in penguins. It is surprising that an increase in catabolism of proteins, a less efficient fuel, at the end of phase II does not result in an immediate rise in the rate of mass loss. The rise remained slight even during phase III, probably related to a further reduction in energy consumption.

Despite the augmentation of proteolysis during phase III, and probably of circulating glucogenic amino acids, the fall in blood glucose level indicated that these substrates no longer met the energetic demand of the animal's metabolism. There was a marked inverse correlation between plasma uric-acid concentration and glycemia ($T = -0.61$, $P < 0.001$). This situation is also found in adult male King Penguin during breeding (Cherel et al. 1988c) and further supports the idea that there is a premortal rise in protein utilization (Felig 1979).

Throughout the fast, but especially during phase III, hematocrit values declined. In domestic geese and in humans, similar decreases have been related to a reduction of erythrocyte volume (Le Maho et al. 1981, Owen 1989), likely to result from an impairment of erythropoiesis.

Interspecific comparisons of mobilization of body reserves.—Compared with domestic geese, Greater Snow Geese needed more time (32% vs. 8% of the total fasting length) to attain the economical phase II of fasting. Plasma uric-acid values of Greater Snow Geese during phases II and III were higher than in domestic geese (Robin et al. 1987) and even higher than in King Penguin chicks (Cherel and Le Maho 1985, Cherel et al. 1987). Furthermore, the small increase in levels of uric-acid and circulating plasma proteins during the later part of phase II suggests that protein sparing was not as efficient. This is probably related to an increasing metabolic demand for glucose, particularly in the brain, because β-OHB was simultaneously decreasing rapidly. Thus, it can be concluded that Greater Snow Geese did not succeed as well as these other fasting birds in sparing their protein reserves.

Adaptive value of fasting in Greater Snow Geese.—Greater Snow Geese may face periods of food deprivation during incubation, a common occurrence in many geese (Ryder 1970, Ankney and MacInnes 1978, Thompson and Raveling 1987). In nesting anatids, Thompson and Raveling (1987) have suggested that the level of reserves remaining after egg laying determines how the female will allocate her time between nest attentiveness (which increases nesting success) and feeding recesses (which enhance her own survival). The availability of endogenous lipids at the beginning of fasting may limit catabolism of the lean tissues and thus extend the tolerance to fasting (Cuendet et al. 1975, Goodman et al. 1981, Lowell et al. 1986, Robin et al. 1988). In captive Greater Snow Geese, the duration of the fast and loss of body mass were positively correlated to initial lipid reserves, and the two birds that died after fasting had exhausted their lipid stores.

Afton (1979, 1980) and Harvey et al. (1989) suggested that body size is a limiting factor for the amount of stored body reserves. Compared to domestic geese, which spontaneously fast throughout the reproductive period (100 days in females and 75 days in males; Robin et al. 1987), captive Greater Snow Geese tolerated only 34 days of fasting (range 19-42 days). Domestic geese store and carry greater proportions of fat than Greater Snow Geese, because they are twice as large and they do not have to fly. Thus, during a fast long enough to produce a similar loss of body mass (~40% of initial mass), domestic geese can rely almost exclusively on their lipid stores, with fat accounting for as much as 94% of their energy expenditure (Le Maho et al. 1981) in comparison to only 72% in fasting Greater Snow Geese.

Our results suggest that Greater Snow Geese should possess a minimum of 16% of their body mass in fat reserves to sustain total food deprivation throughout a 24-day incubation. During this period, geese would lose up to 30% of their initial body mass and reach the end of phase II of prolonged fasting. However, three factors may influence the fasting endurance of wild Greater Snow Geese: (1) the initial body mass and fat reserves of the birds; (2) their hormonal status; and (3) environmental conditions. It is possible that the hormonal status prevailing during the reproductive period may decrease the requirement for energy reserves during fasting by facilitating a faster transition to the economical phase (phase II). In contrast, predation, intraspecific competition, and exposure of the eggs and parents to inclement conditions are factors that should increase the energy requirement of incubating birds.

At the beginning of incubation, wild Greater Snow Geese have smaller fat reserves (a mean of 10% of the body mass or 253 g for females,

and 3% or 95 g for males; L. Choinière, pers. comm.) than captive birds, and less than female Lesser Snow Geese at the same stage (Ankney and MacInnes 1978). These results suggest that female Greater Snow Geese withstand only a partial fast during the incubation period, whereas males may not fast at all.

ACKNOWLEDGMENTS

We thank Helga Guderley for advice and for lending her spectrophotometer during laboratory analyses, and Claude Lavoie for assistance during experiments. Additional technical help was provided by the employees of the Animalerie du Pavillon des Services, Université Laval, and of the Zoo de Charlesbourg (Québec) during the 2.5 months the geese were held in captivity. Austin Reed and an anonymous reviewer offered valuable suggestions for the manuscript. This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada to G. Gauthier and J. Larochelle, and a grant from le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche du Québec to G. Gauthier.

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