EFFECT OF HATCHING DATE ON BODY AND ORGAN DEVELOPMENT IN GREATER SNOW GOOSE GOSLINGS[1]

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Abstract. Growth rate in geese is sensitive to the feeding conditions during the brood-rearing period, and late-hatched goslings grow at a lower rate than early-hatched ones. We examine how the seasonal decline in food supply affected the development of body components of late-hatched and early-hatched goslings in male and female Greater Snow Geese (*Chen caerulescens atlantica*). We collected and autopsied 48 early-hatched (EH, mean age at capture = 42.4 days) and 48 late-hatched goslings (LH, mean age = 34.8 days), divided equally among sexes, near fledging at four different sites on Bylot Island, Northwest Territories. After statistically adjusting for differences in body size between the two groups, EH goslings had more body protein than LH ones. However, the development of all organs was not affected equally. The mass of most supplying organs (the food acquisition apparatus: legs, esophagus, intestine, and liver), which develop early during growth, was similar between EH and LH goslings. In contrast, LH goslings had much smaller breast muscles than EH goslings, even after adjusting for size differences. Body fat was very low and similar in both groups. Body mass, body protein, intestine, and breast muscles showed a sexual dimorphism favoring males in EH, but not in LH, goslings. These results show that poor feeding conditions encountered by LH goslings disproportionately affected late-developing organs compared to early-developing ones, and males compared to females. Differences in organ development could reflect an adaptive response to reduced food availability. Prioritizing the development of supplying organs at the expense of other organs when food availability is low could help goslings maintain a high nutrient intake.

Key words: breast muscle, Chen caerulescens atlantica, *digestive tract, Greater Snow Goose, growth, hatching date, organ development, sexual dimorphism.*

INTRODUCTION

Timing of reproduction is an important determinant of reproductive success in birds. Young fledging early in the season generally have better survival and a higher probability of recruitment into the population than those fledging late (Cooke et al. 1984, Hochachka 1990, Spear and Nur 1994). The timing of fledging is dependent upon both the timing of hatch and the growth rate of young. Thus, we would expect strong selection for fast growth rate, especially in large birds with short breeding seasons and long migrations, such as geese.

Precocial birds face particular problems during growth: their self-feeding mode increases maintenance cost for locomotion and thermoregulation, and requires a high proportion of mature tissues in organs, such as legs, in order to obtain food. Precocial young thus are faced with the delicate problem of optimally allocating their resources between body maintenance and devel-

opment of various body components. This may result in trade-offs: for instance, a rapid development of legs may facilitate food finding and escape from predators, but it may slow down overall growth and delay fledging (Ricklefs 1979). Such trade-offs also may vary seasonally depending upon environmental conditions.

Growth in geese is highly sensitive to seasonal variations in environmental conditions and this may have strong fitness consequences. Late-hatched goslings grow more slowly (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994), become smaller juveniles and adults (Larsson and Forslund 1991), have a lower probability of survival during migration (Owen and Black 1989, Schmutz 1993, Williams et al. 1993), and a lower probability of recruitment into the breeding population (Cooke et al. 1984) than early-hatched ones. Poor feeding conditions encountered by late-hatched goslings are largely responsible for their slow growth (Lindholm et al. 1994, Lepage et al. 1997). During the arctic summer, goslings are in presence of food which declines rapidly in quality (Sedinger and Raveling 1986, Manseau and Gauthier 1993). Fur-

thermore, late-hatched goslings may suffer from a depletion of vegetation by early-hatched goslings in high quality habitats (Gauthier et al. 1995, Lepage et al. 1997).

Cooch et al. (1996) showed that male Lesser Snow Geese (Chen caerulescens caerulescens), which are slightly larger than females, suffer a proportionally larger seasonal decrease in fledging mass compared to females when faced with poor feeding conditions. No sex differences were found in body size, which suggests that growth of soft tissues suffered more from a low food supply. Because late-hatched goslings have less time to grow and a lower food supply than early-hatched ones (Lepage et al. 1997), it could be adaptive for them to modify the growth pattern of various organs to maximize their probability of survival. The growth pattern in geese is characterized by very early development of leg muscles and the digestive tract, whereas the development of breast muscles, the largest muscle mass in adults, is delayed until shortly before fledging (Sedinger 1986, Lesage and Gauthier 1997). Prioritizing development of legs and digestive tract could be advantageous when food is declining in quality and quantity. However, if time available for growth is limiting, late-hatched goslings also may benefit from initiating development of breast muscles at an earlier stage of development than early-hatched ones in order to speed up fledging.

In this study, we examined variations in the development of various body components in relation to hatching date and sex in Greater Snow Geese (C. c. atlantica). Our objectives were to determine (1) how the seasonal decline in food supply affected body and organ development of late-hatched goslings compared to early-hatched ones, and (2) if seasonal variations in development differed between females and males.

METHODS

STUDY AREA

The study was conducted at the Bylot Island National Wildlife Refuge, Northwest Territories, Canada (73°N–80°W). This island is the most important nesting colony of Greater Snow Geese with over 30,000 nesting pairs in 1993 (Reed et al. 1992; unpubl. data). The study area is centered in the lowlands of a glacial valley (50 km²) on the south plain of the island and is characterized by wet polygon tundra (Gauthier et al.

1995). The wetlands (Pond/Lake and Wet Meadow; Fig. 1) are dominated by graminoids such as Dupontia fisheri, Carex aquatilis var. stans, Eriophorum scheuchzeri, and E. angustifolium (Hughes et al. 1994a) which are the most important food of geese. The lowlands are surrounded by hills with moist upland tundra.

COLLECTING METHODS

Four banding drives were carried out over a 6-day period just before fledging in 1993 (Fig. 1). Each capture site was selected based upon the presence of large flocks of molting geese with young. These flocks (400–600 geese) were surrounded by people and then slowly pushed into large pens. The four sample sites were independent of each other. Indeed, among all goslings banded and released at the four sites (n = 1,359), only one site involved the recapture of five goslings banded at previous sites: three goslings banded at site 1, and two banded at site 2 were recaptured at site 4 (see Fig. 1).

All geese captured were sexed by cloacal inspection, measured (length in mm of culmen, head, tarsus, and 9th primary), weighed, and banded. At each capture site, a total of 24 goslings were sacrificed among early and late-hatched goslings (n = 12 in each group, equally divided between each sex). Early and late-hatched goslings were those > 2 days older or younger, respectively, than the median age of all goslings caught at each site. Sacrificed goslings were chosen randomly among those that met the age criteria (based upon 9th primary length; see below) as birds were processed during the banding operation. The 24 collected goslings came from a large sample of goslings caught at each site (range: 256–425; Table 1).

Age of goslings was estimated using 9th primary length (mm) because these two variables are closely related (Lepage et al. 1997) and the 9th primary has a linear growth (Boyd and Maltby 1980, Lindholm et al. 1994). The relationship between age and 9th primary length was determined on a sample of known-age birds, i.e., goslings which were individually web-tagged at hatch in the study area and recaptured at banding. Thus, this relationship was established on birds that had experienced the same growth conditions as the birds that we collected. We estimated age (days) of captured goslings using the linear equation previously determined for the relationship between length of the 9th primary and
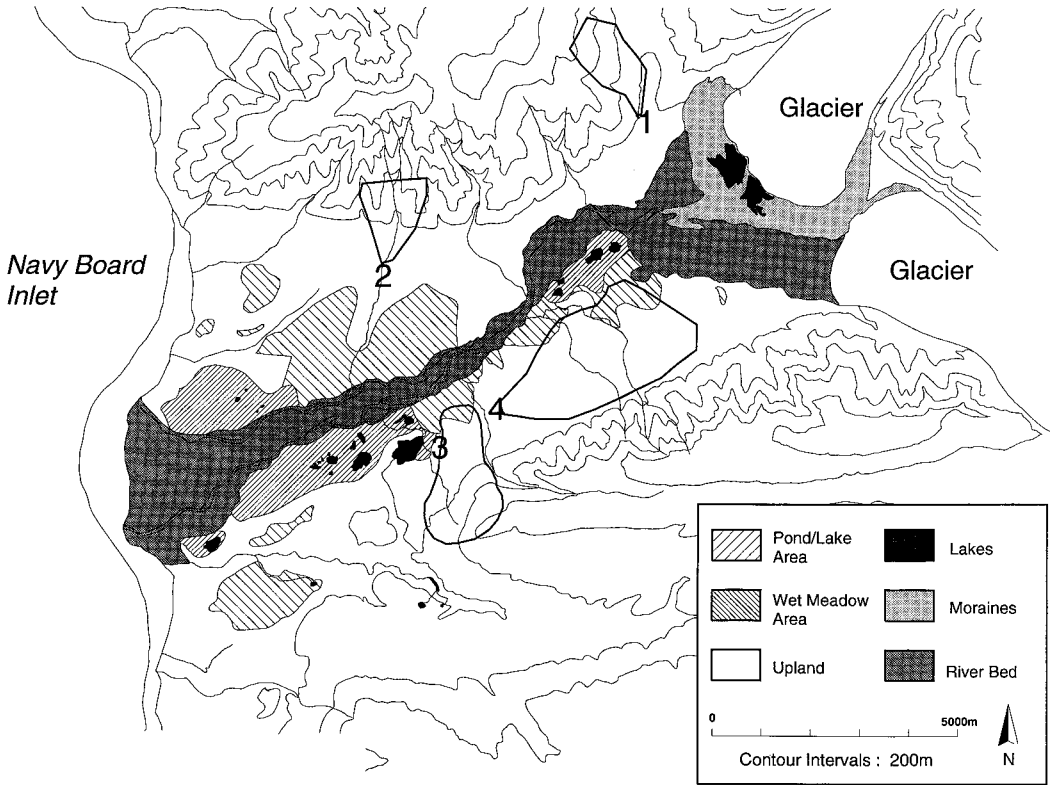
FIGURE 1.   The study area on Bylot Island, Northwest Territories. The bold lines enclose the area where geese were surrounded for capture, and numbers (1 to 4) show locations of pens used at each capture site.

TABLE 1.   Mean age of goslings in the population, age of goslings caught, and age and body ash of early- and late-hatched Greater Snow Goose goslings collected at four different capture sites on Bylot Island, NWT. Sample sizes are in parentheses.

	Site							
	1		2		3		4	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Capture date (August)	9		10		12		14	
Age of goslings (days)								
Population mean[a]	37		38		40		42	
All goslings caught[b,c]	37.6 (425)	0.1	37.1 (304)	0.2	39.3 (291)	0.2	39.8 (256)	0.2
Known-age goslings[d]	36.7 (21)	0.3	37.0 (8)	0.7	39.6 (22)	0.2	40.5 (11)	0.5
Early goslings[b,e]	42.3	0.3	40.8	0.2	43.2	0.2	43.1	0.3
Late goslings[b,e]	34.0	0.7	33.0	0.6	35.2	0.6	36.7	0.3
Body ash (g)								
Early goslings[e]	67.4	2.9	56.4	3.0	55.4	2.5	56.9	2.0
Late goslings[e]	40.8	2.5	35.9	1.7	30.8	2.5	33.8	1.5

[a] Age based upon median hatching date (3 July, n = 367 nests; Gauthier, unpubl. data).
[b] Age estimated using 9th primary length (see Methods).
[c] Excludes known-age goslings.
[d] Age based upon known hatching date (goslings web-tagged at hatch).
[e] n = 12 at each site.

age. Because web-tagged goslings and those that we sacrificed were captured in the same banding drives, data available for the relationship between 9th primary and age increased throughout the study. The equation was updated with each capture. The final equation ($r^2 = 0.62$, $n = 102$, $P < 0.001$; SE of estimate: 1.7 days) was:

Age = 22.81 + (0.0991 × 9th-primary length)

Early and late-hatched goslings were those with a 9th primary > 20 mm longer or shorter, respectively, than the median length of all goslings caught on each day, because the average growth rate of the 9th primary was 10.1 mm day^{-1}.

BODY COMPOSITION ANALYSES

We autopsied the birds in the field, removing the following organs in each bird: left breast muscles (pectoralis major and supracoracoideus), left leg muscles (including all muscles originating along the femur or the tibiotarsus), the esophagus (with the proventriculus), gizzard, liver, and intestine. The content of the digestive tract was removed and its weight subtracted from whole body mass to obtain the ingesta-free body mass. In the laboratory, all tissues were freeze-dried to constant mass, and fat was determined in duplicate, 1-g samples of all tissues using a Rafatec apparatus (Randall 1974). Ash content of the body was determined by incinerating a 3-g dried sample of the carcass (all tissues not removed during the autopsies except for feathers). Protein content of muscles and viscera was estimated using the lean dry mass, and carcass protein using the ash-free lean dry mass. Body fat (or protein; feathers excluded) was calculated by adding the amount of fat (or protein) determined in all tissues analyzed (breast muscles + leg muscles + esophagus + gizzard + intestine + liver + carcass). More details of the methods can be found in Lesage and Gauthier (1997).

STATISTICAL ANALYSES

The relationship between hatching date and organ development could not be directly assessed because we could not sample these variables throughout the entire growing period. However, the effect of hatching date could be assessed indirectly by comparing organ size between early- and late-hatched groups (as defined above). Because early- and late-hatched goslings were collected at different ages (Table 1), we had to adjust for this age difference. However, we contend that adjusting for body size rather than age to compare organ development between the two groups was a better approach. The rationale for doing so is as follows. Because late-hatched goslings grow more slowly than early-hatched ones, they are always smaller than the latter at the same age (Lindholm et al. 1994, Lepage et al. 1997). Hence, if we adjust only for age, organs of late-hatched goslings should still be smaller than those of early-hatched ones because of the overall difference in size between the two. On the other hand, if we correct for body size before comparing organs between the two groups, we will account for both differences in age and seasonal effects on overall size.

The dependent variables used for the analyses were ingesta-free body mass, body protein, body fat, and protein mass of the breast muscles, leg muscles, esophagus, gizzard, liver, and intestine. On all these variables, we performed a two-way factorial ANOVA to examine the effects of sex and hatching group (early or late), using capture site as a blocking variable. We also performed a two-way analysis of covariance (ANCOVA) using total body ash as a covariate to determine if relative development of body components differed between early and late-hatched goslings, after adjusting for differences in body size between the two groups. Because structural size should be more closely related to the skeleton than any other tissues (Moser and Rusch 1988), we chose total body ash as an index of body size.

Use of the ANCOVA requires that several assumptions be met. First, some overlap in body ash values between early and late-hatched goslings is desirable, and this was the case. Second, relationships between the response variables and the covariate should be linear in each sex × hatching-group combination. This assumption was met for all organs except breast muscles, which showed a slight tendency for a nonlinear relationship with body ash at low body ash values. A square-root transformation solved this problem by making the relationship linear.

A third assumption is that the slopes of the regression lines are homogeneous. To test this assumption, we first included in the model a term to account for the interaction between body ash, hatching group, and sex with 3 degrees of freedom. If this interaction was not significant,

TABLE 2. Two-way analysis of variance (F values) of the effect of hatching group (early- and late-hatched birds) and sex on body mass, body protein, protein mass of several organs, and body fat of Greater Snow Goose goslings ($n = 96$) collected near fledging on Bylot Island, NWT. Capture site was included as a block variable in the analysis.

	Site	Hatching group	Sex	Hatching group × sex
Body mass	11.71***	158.2***	9.01**	2.63
Body protein	14.66***	256.6***	12.18***	3.61
Breast muscles	6.98***	511.3***	2.50	3.48
Leg muscles	15.81***	77.02***	2.81	0.19
Esophagus	13.54***	14.87***	4.06*	3.20
Gizzard	0.91	20.65***	6.08*	0.92
Intestine	2.98*	2.04	6.81*	8.94**
Liver	7.71***	2.65	0.74	1.16
Body fat	8.90***	20.70***	1.03	2.02

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

we concluded that homogeneity of slopes was respected and the term was removed from the model. If the interaction was significant, we subdivided it into its three components (body ash × hatching group, body ash × sex, and body ash × hatching group × sex, each with 1 df) and repeated the analysis. In all cases, the interaction of body ash × sex and the 3-way interaction were not significant. We thus retained in the final model only the significant interaction between body ash and hatching group, where appropriate. To explore this interaction, we compared least-squares means of dependent variables between early and late-hatched goslings at the overall mean body ash value, and at values obtained at 25 and 75% of the distribution of body ash data. The 25 and 75% values corresponded closely to the mean body ash of late and early-hatched goslings, respectively. All analyses were performed with SAS (SAS Institute 1985).

RESULTS

AGE OF GOSLINGS AT CAPTURE

The age of the known-age (i.e., web-tagged) goslings captured corresponded well to the estimated age of all goslings caught at the same site (Table 1). Thus, the relationship between age and 9th primary length used to discriminate between early-hatched (EH) and late-hatched (LH) goslings appeared to estimate well the age of goslings at each capture site. The age of goslings caught at sites 1 to 3 was close to the median expected age of the population (based upon median hatching date determined in 367 nests visited at hatching), whereas those caught at site 4 were slightly younger (Table 1). At all capture

sites, EH goslings collected were about 8 days older than LH, except at site 4 where the difference was only 6 days. Overall, mean (± SE) age of EH and LH goslings was 42.4 ± 0.2 days and 34.8 ± 0.3 days, respectively.

EFFECT OF HATCHING DATE AND SEX ON DEVELOPMENT

There was a significant site effect on body mass, body fat, and protein mass of all organs except for gizzard (Table 2). A posteriori tests showed that this was due to the size of goslings captured at site 1, which was larger than at other sites ($P < 0.05$; Table 1). Hatching group had a strong effect on all variables, except intestine and liver (Table 2), as body mass and organs of EH goslings were heavier than those of LH ones. This effect was expected given the 6–8 days difference in age between the two groups. Sex differences were present for body mass, body protein, esophagus, gizzard, and intestine (males being larger than females) but were absent in other organs.

When we included body ash as a covariate in the analyses (i.e., when we adjusted for differences in body size between EH and LH goslings), a significant site effect persisted for all variables except gizzard (Table 3). Differences between EH and LH goslings disappeared for some variables but remained present for body mass, body protein, breast muscles, and gizzard. However, there was some interaction between hatching group and sex, and between hatching group and body ash.

There was a significant interaction between the effects of hatching group and body ash on

TABLE 3. Two-way analysis of covariance (F values) of the effect of hatching group (early- and late-hatched birds) and sex, controlling for body size using body ash as a covariate, on body mass, body protein, protein mass of several organs, and body fat of Greater Snow Goose goslings ($n = 96$) collected near fledging on Bylot Island, NWT. Capture site was included as a block variable in the analysis.

	Body ash	Site	Hatching group	Sex	Hatching group × sex	Hatching group × body ash
Body mass	94.98***	9.41**	17.77***	7.30**	5.94*	13.42***
Body protein	110.2***	9.87***	17.33***	11.57**	7.61**	7.73**
Breast muscles[a]	54.26***	10.20***	42.79***	0.23	3.80*	6.69*
Leg muscles	51.61***	9.58***	0.0	0.72	0.05	—[b]
Esophagus	8.76**	6.70***	0.07	2.43	3.01	—[b]
Gizzard	12.78**	0.47	6.63*	4.42*	1.63	7.19**
Intestine	0.57	3.15*	0.02	5.94*	8.69**	—[b]
Liver	10.21**	4.51**	2.99	0.12	0.98	—[b]
Body fat	29.00***	3.86*	2.67	0.05	1.92	—[b]

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[a] Square-root of variable was used to linearize the relationship between breast muscles and body ash.
[b] The interaction between hatching group and body ash was not retained in the model because the interaction was not significant ($P > 0.05$). In this case, main effects shown were calculated without this interaction term.

body mass because the slope of the relationship between body mass and body ash was steeper in LH compared to EH goslings (Fig. 2). In small goslings (25% body ash value), EH were heavier ($P < 0.05$) than LH ones, but in goslings of average size, the difference was present only in males ($P < 0.05$; Fig. 2). No differences were found between EH and LH in large goslings (75% body ash). The significant interaction between the effects of hatching group and sex on body mass (Table 3) occurred because EH males were heavier than EH females at all gosling sizes ($P < 0.001$), whereas body mass of LH males and LH females was identical (Fig. 2).

For body protein, the significant interaction between hatching group and body ash (Table 3) also was caused by the steeper slope of the relationship between body protein and body ash in LH goslings compared to EH goslings (Fig. 2). Despite this interaction, EH goslings had more body protein than LH goslings ($P < 0.05$) across all ranges of body size, except in large females (75% body ash, Fig. 2). Again, there was a significant interaction between the effects of hatching group and sex because, at all body sizes, EH males had more body protein than EH females ($P < 0.001$), but this difference was absent in LH goslings (Fig. 2).

Development of breast and leg muscles showed interesting differences. Despite a significant interaction between the effects of hatching group and body ash (Table 3), breast muscle mass was much heavier in EH than in LH goslings across all ranges of body size ($P < 0.001$, Fig. 2). The significant interaction between the effects of hatching group and sex (Table 3) occurred because breast muscles of EH males were heavier than those of EH females across all ranges of body size, whereas the reverse was true in LH goslings (Fig. 2). In contrast, after correcting for body size, leg muscle mass did not differ between EH and LH goslings, nor between the sexes (Tables 3 and 4). There was no interaction between the effects of hatching group and body ash on leg muscles.

The pattern of development of all digestive organs was similar, except for the gizzard. The mass of esophagus, intestine, and liver was similar between EH and LH goslings after adjusting for differences in body size (Tables 3 and 4). Also, there were no significant differences between males and females in the mass of esophagus and liver. There was a significant interaction between the effects of hatching group and sex on intestine mass (Table 3) because EH males had heavier intestines than EH females, whereas no differences were found in LH goslings (Table 4). For gizzard, there was a strong interaction between the effects of hatching group and body ash (Table 3) because the slope of the relationship between gizzard mass and body ash was steeper in LH compared to EH goslings (Fig. 2). In small goslings (25% body ash value), EH tended to have heavier gizzards than LH, but the reverse was true in large goslings (75% body ash, Fig. 2). Males had heavier gizzards than females across all ranges of body size in both EH and LH goslings (Fig. 2). Although the sex difference tended to be larger in EH goslings,
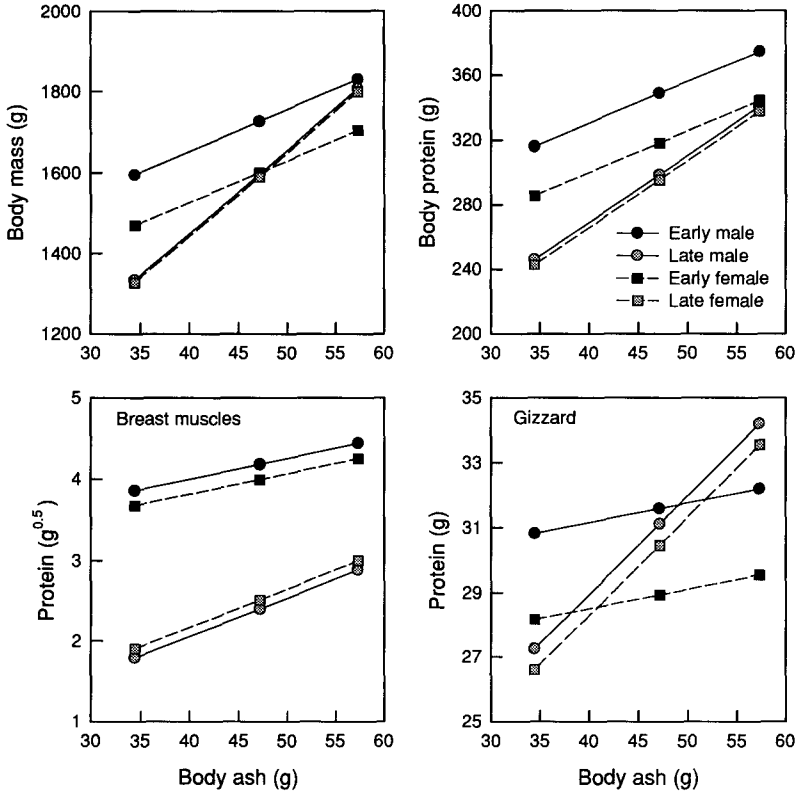
FIGURE 2. Relationship between body components (body mass, body protein, and protein mass of breast muscles and gizzard) and body ash in early- and late-hatched, male and female Greater Snow Goose goslings ($n = 96$) collected near fledging on Bylot Island, NWT. Least-squares mean values are presented for goslings of average body size (at mean body ash value, 47.2 g), and for small and large goslings (values obtained at 25%, 34.4 g, and 75%, 57.3 g, of the distribution of body ash data, respectively). This illustrates the interaction between the effects of hatching group and body ash (see Table 3).

the interaction term between hatching group and sex was not significant (Table 3).

Body fat was similar between EH and LH goslings after correcting for body size, and between males and females (Tables 3 and 4).

DISCUSSION

EFFECT OF CAPTURE SITE

We found differences in gosling size and organ development among capture sites. Other studies

TABLE 4. Protein mass of several organs and body fat (g) according to sex and hatching group (early-hatched and late-hatched) in Greater Snow Goose goslings ($n = 96$) collected near fledging on Bylot Island, NWT. Least-squares means (after correcting for differences in body size; see Methods) are presented.

| | Male | | | | Female | | | |
| | Early | | Late | | Early | | Late | |
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Leg muscles	21.7	0.6	21.5	0.7	21.1	0.6	21.2	0.7
Esophagus	4.7	0.2	4.5	0.2	4.3	0.2	4.6	0.2
Intestine[a]	19.1 a	0.6	17.7 ab	0.5	16.8 b	0.5	17.9 ab	0.6
Liver	10.9	0.5	11.7	0.5	10.4	0.5	12.0	0.5
Body fat	9.7	0.8	10.6	0.7	8.7	0.7	11.3	0.8

[a] Because of a significant interaction between hatching group and sex, comparisons among cell means are presented (means with different letters differ at $P < 0.05$).

have reported effects of habitat on growth in geese (Larsson and Forslund 1991, Aubin et al. 1993). Goslings were largest at site 1, which was the most upland capture site (hillside; Fig. 1). This is surprising because the highest quality habitats (Pond/Lake and Wet Meadow) are found in lowlands (Manseau and Gauthier 1993, Hughes et al. 1994a). The trend for larger goslings in hillsides compared to lowlands could be a consequence of seasonal movements between habitats. In response to food depletion in preferred lowland habitats, families could be forced to use larger feeding areas, or to move to lower quality upland habitats late in the summer (Hughes et al. 1994a, 1994b, Gauthier et al. 1995). This suggests that capture site was not a good indicator of the brood-rearing site used during the summer.

EFFECT OF HATCHING DATE

Hatching of clutches was highly synchronous in 1993 (87% hatched over a 7-day period; Lepage 1997). Despite this high synchrony, our results show that a difference of only one week in hatching date had significant effects on goslings' development at the end of the summer.

Lindholm et al. (1994) experimentally showed that EH goslings grow faster and have a better survival than LH ones. When we accounted for differences in body size using skeletal structure, we found that body protein was generally lower in LH than in EH goslings. This supports the suggestion of Cooch et al. (1996) that "soft tissue" mass (i.e., mostly muscles) is affected more than the skeletal component when growth is reduced. Because protein synthesis is largely dependent upon nitrogen intake (Robbins 1983, Gadallah and Jefferies 1995), our results suggest that the available nitrogen for LH goslings was reduced. Low nitrogen intake by LH goslings was likely a consequence of the seasonal decline in nitrogen and the seasonal increase in fiber concentration of arctic plants (Sedinger and Raveling 1986, Manseau and Gauthier 1993), and of food depletion in preferred feeding areas (Cooch et al. 1993, Lepage et al. 1997).

Poor feeding conditions encountered by LH goslings also could be a consequence of inadequate parental care. Experienced parents nest earlier and, thus, hatch their clutch earlier (Hamann and Cooke 1987, Sjöberg 1994). The higher competitive ability of more experienced parents also may enhance their access to higher

quality habitats when settling into a brood-rearing area (Hughes et al. 1994b). However, this hypothesis was not supported by the clutch manipulation experiments conducted by Lepage (1997), which indicated that differences in parental quality explained little of the seasonal variation in gosling growth.

How did the reduction of body protein in LH goslings affect their allocation of internal resources during the development of various body components? The development of all organs was not affected equally. The organs important for acquiring nutrients during growth (legs, esophagus, intestine, and liver, with exception of the gizzard perhaps) developed at similar rates in EH and LH goslings when differences in body size were accounted for. In contrast, after adjusting for size differences, LH goslings had much smaller breast muscles than EH goslings. This result is consistent with our earlier finding (Lesage and Gauthier 1997) that breast muscles, the largest muscle mass in adults, are one of the last organs to develop in goslings. We suggest that this pattern of development could represent an adaptive response of the LH goslings to poor feeding conditions. Prioritizing the development of "supplying" organs (i.e., the food acquisition apparatus) at the expense of other organs when food quality and quantity is poor could help goslings maintain a high nutrient intake. When supplying organs have reached a critical size, other organs could then increase their rate of development. A consequence of this strategy was that growth of the late-developing breast muscles was disproportionately affected. It follows that a delay in development of breast muscles could delay fledging. Thus, although this strategy may maximize the chances of survival of goslings in the short term, it is unclear how it would benefit them in the long term when one considers the importance of fledging as early as possible on subsequent survival probability in geese (Cooke et al. 1984).

An alternative explanation is that the observed pattern of organ development, rather than being an adaptive response by goslings, resulted from constraints imposed by the seasonal decline in feeding conditions (Cooch et al. 1996). Lepage et al. (1997) showed that variations in gosling growth was best explained by the availability of nitrogen in their food during the period of fastest growth (i.e., between 11 and 25 days of age). It is possible that, in the first 10 days

after hatching, feeding conditions had not deteriorated to the point of preventing optimal growth in LH goslings. Under this scenario, early-developing supplying organs of LH goslings could grow normally during the earlier period of growth. In contrast, late-developing organs such as breast muscles would grow poorly because of poor feeding conditions encountered later in the summer.

Body fat was very low and similar in both groups. This shows that fat accumulation in preparation for the fall migration had not started in either group. However, by fledging earlier in the season, EH goslings would have more time available than LH ones to complete development of their flight muscles and accumulate fat for migration (Lesage and Gauthier 1997), thus enhancing the chances of post-fledging survival.

EFFECT OF SEX

Adult males are about 11% heavier than females in Greater Snow Geese (data from birds in early March, the period of minimum body mass in their annual cycle; Gauthier at al. 1992). When accounting for differences in body size, a sexual dimorphism in body mass favoring males was present in EH goslings, but absent in LH ones. Although this suggests that poor feeding conditions encountered by LH goslings disproportionately affected males compared to females (a result also found by Cooch et al. 1996), we did not detect sexual dimorphism in all organs examined. Sexual dimorphism was found for body protein, intestine, breast muscles, and gizzard in EH goslings, but was reduced or absent in LH goslings. Breast muscles even showed a trend for a reverse size dimorphism in LH goslings. Although the reduced sexual dimorphism of late-developing organs in LH goslings was consistent with the hypothesis of poor feeding conditions late in the season, reduced sexual differences in the size of early-developing organs such as intestine and gizzard in LH goslings was not consistent with this hypothesis. The latter response of some early-developing organs argues against the hypothesis that growth patterns observed in LH goslings were a simple consequence of reduced food availability later in the summer, and thereby favors the hypothesis of an adaptive response.

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