EFFECTS OF HATCH DATE AND FOOD SUPPLY ON GOSLING GROWTH IN ARCTIC-NESTING GREATER SNOW GEESE[1]

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Abstract. We studied the effects of hatch date and food supply on growth of goslings of the Greater Snow Goose (*Chen caerulescens atlantica*) at Bylot Island, Northwest Territories, Canada. Two groups of goslings were collected and imprinted on humans, one early ($n = 15$) and one late ($n = 19$) in the hatching period (span of 5–7 days). Early and late-hatched groups were each divided into food supplement and control treatments. Goslings from control groups fed exclusively on natural vegetation throughout the summer whereas those from the food-supplemented groups had access to a high-protein commercial diet for 12 hr each day. Early-hatched goslings grew faster, and were heavier and larger at 40 days (near fledging) than late-hatched goslings. Food-supplemented goslings also grew faster, and were heavier and larger at 40 days than controls. Plumage (9th primary) developed at a younger age when goslings hatched early or received a food supplement but plumage growth rate was constant among groups. Early-hatched goslings survived better than those hatched late, irrespective of feeding treatment. More late-hatched, food-supplemented goslings survived than late-hatched controls, but the difference was not significant. Goslings that were lighter than the mean were more likely to die than heavier ones at any given age. We conclude that differences in growth and possibly survival between early and late-hatched goslings are food-mediated and largely caused by the rapid decline in quality of arctic plants during the summer. Differences as small as 5–7 days in hatch dates may have major fitness consequences in arctic-nesting geese.

Key words: *Food experiment; timing of breeding; growth rate; survival; hatch date; Arctic; Chen caerulescens; Snow Geese.*

INTRODUCTION

Early growth in birds may have important fitness consequences. Conspecific young that grow slowly and fledge with below average body mass have relatively low survival rates (e.g., Owen and Black 1989, Tinbergen and Boerlijst 1990, Magrath 1991). Final body size in birds is strongly affected by environmental conditions during growth (James 1983, Boag 1987, Richner 1989, Larsson and Forslund 1991, Cooch et al. 1991a, 1991b). For instance, young hatched late in the season often have slower growth or lower survival than those hatched earlier (Perrins 1965, Newton and Marquiss 1984, Alatalo and Lundberg 1986), and

this is commonly associated with reduced food availability late in the season (Perrins 1965, van Balen 1973, Alatalo and Lundberg 1986, Magrath 1989, van Heezik and Davis 1990).

The relationship between hatch date, growth and survival of young has received considerable attention in arctic-nesting geese because these large, precocial birds are confronted with a very short breeding season, a consequence of their high breeding latitude. In geese, late-hatched goslings often grow more slowly (Cooch et al. 1991a, Sedinger and Flint 1991), which increases their risk of not completing their growth in time for the southward migration. In addition, late-hatched goslings become smaller juveniles and adults (Cooch et al. 1991a, Larsson and Forslund 1991), have higher mortality during the autumn migration (Owen and Black 1989), and are recruited into the breeding population at a lower rate (Cooke et al. 1984).

Goslings are obligate herbivores, depending almost entirely on plant nutrients for their growth (Sedinger and Raveling 1984, Manseau and Gauthier 1993). Primary productivity is low in the

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arctic (Bliss et al. 1973), but plants have relatively high nitrogen and low fiber content compared to plants at more southern latitudes in the summer (Manseau and Gauthier 1993). Although grazing may increase nitrogen levels in plants used by goslings, both grazed and ungrazed plants undergo a pronounced seasonal decline in nitrogen and increase in fiber content as they complete their life cycle (Gauthier, unpubl. data). Therefore, growing goslings are faced with a food source of declining quality during the summer (Sedinger and Raveling 1986, Manseau and Gauthier 1993). Because of their colonial nesting habits and gregariousness, geese may also overgraze their habitat which further deteriorates the feeding conditions of late-hatched goslings (Sedinger and Raveling 1986, Cooch et al. 1991b). Based on this evidence, authors have linked the slower growth rate of late-hatched goslings to the decrease in food quality and availability over summer (Cooch et al. 1991a, 1991b, Sedinger and Flint 1991, Larsson and Forslund 1991). These studies, however, have not ruled out the effect of differential parental care on gosling growth between early and late breeders (Prop et al. 1984).

In this study, we experimentally manipulated the food supply of goslings during the growing period while controlling parental care to test the hypothesis that lower quality food experienced by late-hatched goslings is responsible for their reduced growth compared to early-hatched ones. The field experiment was conducted on Greater Snow Geese (*Chen caerulescens atlantica*), one of the northernmost breeding geese in North America.

STUDY AREA AND METHODS

This study was conducted in 1991 on Bylot Island (73°08′N, 80°00′W), Northwest Territories, Canada. The study area is a 12-km-long glacial valley that extends to the sea. In 1991, over 1,000 Greater Snow Goose pairs nested and reared their young within the valley. The lowlands of the valley are dominated by shallow sunken polygons that form numerous small ponds of irregular shape. The edges of ponds and lakes form wet, freshwater meadows dominated by *Dupontia fisheri, Carex aquatilis* var. *stans, Eriophorum scheuchzeri* and *E. angustifolium* (Gauthier and Tardif 1991, Hughes et al. 1994). The 24-hr daylight period extends from early May to early August.

FIELD METHODS

We conducted extensive nest searches during the laying, incubation, and hatching periods. Goslings ($n = 348$) were web-tagged in 121 nests at hatch. We weighed each gosling and measured the lengths of their tarsus, head and culmen. In addition, hatchlings of intermediate mass (relative to brood) were collected, one per nest, for the experiment. The first group of goslings was collected 2–3 days before the median hatch date (early-hatched group) and a second group 3–4 days after the median (late-hatched group; Fig. 1). All birds used in the experiment were collected within 24 hr after hatching (except for one individual of the "early" group that was collected on 5 July while still inside a cracked egg) and taken to the field camp immediately after collection. Humans cared for goslings 24 hr each day to facilitate imprinting. During the first three days, the goslings were housed in two 66 × 42 × 29 cm boxes and provided with commercial duck starter (Purina Game Bird Breeder Startena, min. 30% protein, 2.5% crude fat, max. 7% fiber) and water. Goslings were taken outside to forage on natural plants for an increasing number of hours each day.

When the oldest goslings within each group reached the age of four days, each individual was sexed by cloacal inspection (the sex of all surviving goslings was confirmed at age 34 days). Captive goslings surviving to four days (early-hatched, $n = 15$; late-hatched, $n = 19$) were then matched for sex and mass into pairs within each group, and one member of each pair was randomly assigned to the food-supplemented group, the other to the control.

Goslings from the two food-supplemented groups (early-hatched [EF] and late-hatched [LF]) spent 13.7 ± 0.5 and 12.0 ± 0.7 (SE) hr/day outside, respectively, foraging on natural food. They spent the rest of the day (usually between 22:00 and 10:00) in separate wire-mesh cages measuring 125 × 62 × 50 cm and provided with ad libitum water and duck starter chow. The cages were housed in an unheated tent which allowed us to leave goslings unattended. The difference in hours spent outdoors between early and late-hatched goslings was due to rainy weather conditions which occasionally prevented us from taking out the youngest set of goslings (LF). Although LF goslings spent a mean of 1.7 hr/day more in cages with supplemental food than EF
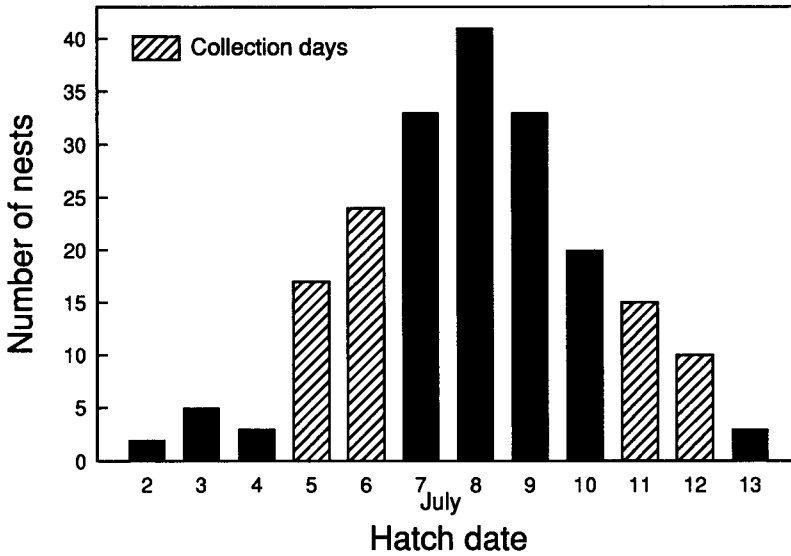
FIGURE 1.   Frequency distribution of hatch dates at the Bylot Island Greater Snow Goose colony, 1991.

goslings, the cumulative daily consumption of duck chow per goose did not differ between early and late-hatched groups (Kolmogorov-Smirnov test, $P = 0.7$). Around 10–12 days, we replaced the "duck starter" chow by a coarser chow (Purina Game Bird Breeder Layena, min. 20% protein, 2.5% crude fat, max. 7% fiber). Food provisioning continued until 40 days.

Goslings in the early control (EC) group spent 19.9 ± 0.6 hr/day outdoors foraging, slightly more than those in the late control group (LC), 19.2 ± 0.9 hr/day. They spent the remaining hours in cages without food for short periods (<2 consecutive hours) when they could not be supervised, and occasionally during periods of foul weather. Goslings in the control group fed exclusively on natural vegetation with the following exceptions. Owing to bad weather, goslings from the LC group had access to duck starter for 27 hr when 7–8 days old, again at age 13–14 days for 48 hr, and for 10.5 hr at age 37–38 days. Goslings from the EC group also had access to chow for 4 hr at the age of 19–20 days. We provided these additional feedings because we believed that some goslings might die of exposure if left to forage during inclement weather.

While outside, all goslings foraged on vegetation in one large, loose flock. The flock was led to grazing areas commonly used by families of wild geese, generally wet meadows which con-

tained a high proportion of *Eriophorum* spp., the food plants of highest quality for goslings (Manseau and Gauthier 1993). Goslings ranged freely while foraging, but were continuously supervised by humans. Late-hatched goslings were taken to the same general area that early-hatched goslings had used at the same age to ensure that food plants available were similar among experimental groups (Manseau and Gauthier 1993). Captive goslings used an area of up to 1 km² around our camp for foraging. Wild geese rarely used this area that summer because we were present with captive goslings for almost 24 hr per day and wild geese retreated at our approach from far away. Hence, grazing on the area used by captive goslings was light compared to the grazing intensity normally encountered on the preferred brood-rearing habitats on Bylot Island (Gauthier, unpubl. data). We thus conclude that natural food was still plentiful for late-hatched goslings. Goslings consumed mainly leaves of *Eriophorum* spp. and *Dupontia fisheri*, with some *Astragalus alpinus* and *Oxytropis* spp. when very young, and also *Carex aquatilis* when near adult size. These plants constitute the main diet of wild Greater Snow Geese during the breeding period (Gauthier 1993, Manseau and Gauthier 1993). Goslings, when 2–3 days old, occasionally consumed mosquitoes. Although predators were often seen (e.g., Arctic fox *Alopex lagopus* and Long-

tailed Jaegers *Stercorarius longicaudus*), no gos-
lings were preyed upon.

MEASUREMENTS

Goslings were measured at the same time by the
same observer each day for the first 12 days, then
on alternate days to the age of 36 days, with an
additional measurement at age 40 days. A final
measurement of early-hatched goslings at the age
of 45–46 days was made. The experiment ended
upon departure from the field site when late-
hatched goslings had reached 40 days of age. Tar-
sus, head, and culmen lengths were measured
with a caliper (±0.1 mm), and length of the ninth
primary feather, an index of plumage develop-
ment, was measured with a ruler (±1 mm) after
the feather emerged from the shaft. Body mass
was determined with an electronic balance to
1.10 kg (±1 g), while heavier birds were weighed
with a 6 kg (±25 g) spring scale. Daily air tem-
peratures (maxima, minima) were recorded.

A series of banding drives was carried out just
before the fledging period of wild goslings from
13 to 21 August, a time when adults were in molt.
Our aim was to recapture families with goslings
that had been tagged at hatching to compare
growth between wild and captive-reared gos-
lings. Head, culmen, tarsus, body mass and ninth
primary were measured, and sex was determined
for 1,041 captured juveniles. Only 17 web-tagged
goslings from a total of nine broods were recap-
tured.

STATISTICAL ANALYSES

Analyses of variance were used to test the effect
of hatch date and food supplement on the mea-
surements of goslings at the age of 40 days. Be-
cause culmen, head and tarsus length were highly
correlated within individuals ($r > 0.98$), an index
of structural size was derived from the data by
principal component analysis (Freeman and
Jackson 1990). The first principal component
(PC1) accounted for 99% of the variance in the
original measures, and weightings were similar
for the three morphometric measurements. Body
mass and PC1 were compared among treatments
(hatch date and food addition) by two-way ANO-
VA. We fitted morphometric data for individual
goslings to a logistic growth model (Ricklefs 1983)
using the iterative nonlinear least squares esti-
mation technique. A logistic regression analysis
was used to examine the relationship between
experimental treatments and survival between

the ages of 4 and 40 days (excluding one acci-
dental death), and the relationship between gos-
ling mass, size, and the probability of survival.
Logistic regression permits analysis of the rela-
tionship between a dichotomous response vari-
able (e.g., dead/alive) and independent variables
(Christensen 1990). The model we used was $P =
1/(1 + e^{-Z})$, where P = probability of survival
and $Z = B_0 + B_1X_1 + B_2X_2 + \ldots + B_pX_p$, where
Bs are the regression coefficients calculated by
maximum likelihood and Xs are the independent
variables. For mass and size analyses, goslings
were classified according to the residuals of mass
and size (PC1) based on growth curves within
each group, at the last measurement before death.
Mass and size were treated as dichotomous vari-
ables (above or below group mean). Dichoto-
mous residuals were more useful than actual de-
viations from the mean because they remained
unchanged for each individual throughout the
experiment and were not influenced by occa-
sional decreases of mass just before death.
Changes in deviance (estimated by χ^2) were used
to test the independent contribution of each fac-
tor included in the model.

RESULTS

GROWTH

At the age of 4 days, variances in mass and size
(PC1) among the four treatments accounted for
little of the total variance ($R^2 < 0.1\%$ and $R^2 =
0.8\%$, respectively). At the age of 40 days, how-
ever, large differences were apparent (Figs. 2 and
3; Table 1). Differences among treatments then
accounted for 73.8% of the total variance in mass
and 75.2% of the variance in size. The mean body
mass of goslings from the EF group was twice
that of the LC group. Goslings from the LF group
grew to a mean size intermediate to that of EF
and EC goslings, but with higher variance. Mean
mass of wild goslings was similar to that of EC
goslings whereas size was intermediate between
EC and LF goslings. The range of values en-
countered in wild birds of similar age exceeded
the range of all the experimental groups com-
bined (except for mass of food-supplemented
goslings, Table 1).

Gosling growth was not completed at 40 days
of age (Fig. 2). The tarsus apparently reached an
asymptote for the fastest-growing goslings (EF),
but head and culmen were still growing. Between
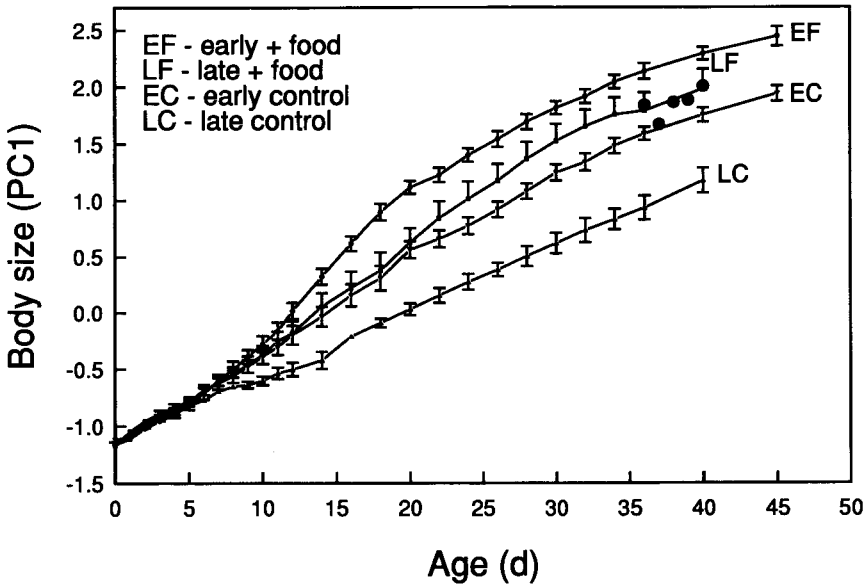40 and 45 days of age, the body mass of goslings

FIGURE 2.   Change in body size (PC1) of captive-reared Greater Snow Goose goslings, in four treatment groups. Culmen, tarsus and head lengths were used for the calculation of PC1. Large dots represent data from 1991 wild goslings ($n = 1,041$). Vertical bars represent standard errors.

in the EF group decreased slightly after we stopped providing food (Fig. 3).

Two-way analysis of variance of gosling measurements at 40 days of age indicated a highly significant effect of both hatch date and food supplement on mass (hatch date, $F = 14.2$, df = 1, 19, $P < 0.003$; food, $F = 34.6$, df = 1, 19, $P < 0.002$) and PC1 (hatch date, $F = 15.2$, df = 1,

19, $P < 0.002$; food, $F = 36.0$, df = 1, 19, $P < 0.001$). There were no significant interactions between hatch date and food supplement effects (all $P > 0.2$), implying that the effects of food supplementation on gosling mass and size at 40 days were similar on early and late-hatched goslings. "K" parameters of the logistic growth functions (an index of growth rate) revealed identical pat-

TABLE 1.   Mean measurements of captive-reared Greater Snow Goose goslings at 40 days of age and of wild goslings at a mean age of 38.3 days. EF = early-hatched + food supplement, EC = early control, LF = late-hatched + food supplement and LC = late control.

|	EF	EC	LF	LC	Wild
n	6	6	5	3	1,041
Mass (g)	2,580	1,880	2,150	1,260	1,759
SE	100	70	190	150	6.1
range	2,230–2,920	1,620–2,180	1,550–2,530	1,180–1,550	750–2,450
Tarsus (mm)	87.5	80.9	82.0	73.5	83.0
SE	1.4	1.9	1.8	2.9	0.1
range	84.2–93.0	75.9–84.8	78.9–86.7	68.7–78.8	65.6–95.2
Head (mm)	112.6	101.4	107.3	90.6	104.7
SE	1.0	1.4	3.7	1.4	0.2
range	108.9–115.5	95.6–106.2	96.8–117.6	88.7–93.2	61.5–122.0
Culmen (mm)	55.3	48.9	52.0	41.4	50.0
SE	0.7	0.9	2.4	1.1	0.1
range	53.0–56.7	46.0–51.9	45.0–57.6	40.0–43.5	36.2–60.8
9th prim (mm)	167.2	131.7	124.6	64.3	157.9
SE	4.3	8.5	19.5	7.9	0.9
range	155–181	93–148	63–165	55–80	0–221
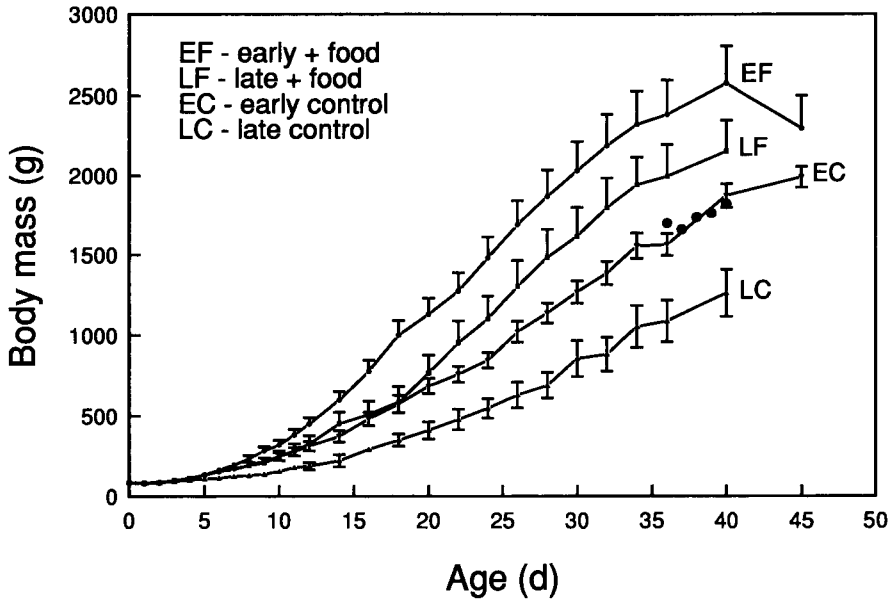
FIGURE 3.   Changes in body mass of captive-reared Greater Snow Goose goslings, in four treatment groups. Large dots represent data from 1991 wild goslings ($n = 1,041$). Vertical bars represent standard errors.

terns (Table 2) to those based on comparison of body measurements at 40 days of age. We did not analyze "K" parameters further because many goslings had not quite reached their final size at the end of the experiment and this may influence parameter estimates (Ricklefs 1983). Size differences between male and female goslings are negligible even at 40 days of age (in wild-caught goslings, difference of $<3\%$, $n > 400$ for each sex; Gauthier unpubl. data). Sexes were also represented in equal proportions among treatment groups, and mortality affected both sexes. Thus, sexual size dimorphism should not affect our experimental results.

DEVELOPMENT OF NINTH PRIMARY AND FLEDGING

The ages at emergence of the ninth primary were 22.3 ± 0.3 days (mean $\pm$ SE, EF), 27.0 ± 1.1 days (EC), 26.3 ± 2.3 days (LF), and 34.7 ± 0.7 days (LC). Hatch date and food supplementation had significant effects on emergence date but no significant interaction was found between the two effects (hatch date, $F = 12.3$, $P < 0.004$; food, $F = 15.4$, $P < 0.002$; hatch date $\times$ food, $F = 1.3$, $P > 0.2$; all df $= 1$, 17). Inspection of residuals showed that growth of the ninth primary was linear, thus allowing direct comparisons of

primary growth among treatments. Daily primary growth was similar ($P > 0.05$) among the four groups: 7.65 mm/day for goslings in the EF group, 7.73 in EC, 7.82 in LF and 6.77 in LC (the last based on $n = 3$).

On the day of emergence of the ninth primary, body masses of goslings were greater in fed than in corresponding control groups (food, $F = 9.4$, $P < 0.01$; hatch date, $F = 0.11$, $P > 0.05$; hatch date $\times$ food, $F = 0.07$, $P > 0.05$; all df $= 1$, 17) and tarsus length differed even more greatly (food, $F = 19.7$, $P < 0.001$; hatch date, $F = 4.3$, $P < 0.06$; hatch date $\times$ food, $F = 0.2$, $P > 0.05$; all df $= 1$, 17). In all groups, ninth primary development began when the tarsus reached about 90% of asymptotic length (using tarsus length at 40 days as an estimate), whereas no relationship

TABLE 2.   Mean fitted K parameters of the logistic growth curve of captive-reared Greater Snow Goose goslings in four treatment groups (see Table 1 for treatments).

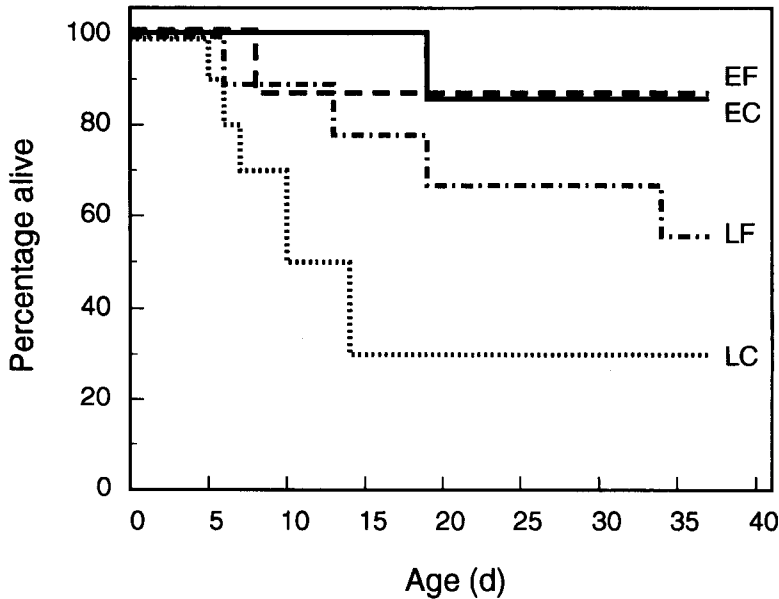|	EF	EC	LF	LC
Mass	0.168	0.110	0.132	0.097
Tarsus	0.109	0.070	0.070	0.036
Head	0.063	0.050	0.045	0.032
Culmen	0.076	0.060	0.057	0.041

FIGURE 4.   Mortality of captive-reared Greater Snow Goose goslings in four treatment groups. EF = early hatched, food supplement (initial $n = 7$); EC = early control ($n = 7$); LF = late hatched, food supplement ($n = 9$); LC = late control ($n = 10$).

was apparent between body mass at the age of primary emergence and mass at 40 days of age (Table 3). However, tarsus development was closer to an asymptote by age 40 days than body mass.

Two goslings in the EF group were first observed to fly at the age of 40–41 days. By 45–46 days of age, six of the early-hatched goslings could fly at least several hundred meters. None of the late-hatched goslings were known to have fledged by age 40 days when we left the field site.

MORTALITY

Mortality of captive-reared goslings was unevenly distributed among groups (Fig. 4). After controlling for the effect of food supplementation, early-hatched goslings survived significantly better than late-hatched goslings (Table 4a). However, food supplementation did not affect survival after accounting for hatch date. Goslings in better condition (i.e., that were heavy relative to their group's mean when the effect of size was controlled for) survived significantly better than

TABLE 3.   Mean mass and tarsus measurements of captive-reared Greater Snow Goose goslings on the date of emergence of the ninth primary feather, and percentage of growth attained (in relation to that at 40 days of age) in four treatment groups (see Table 1 for treatments).

Group	Mass (g)	SE	% Mass at 40 days	Tarsus (mm)	SE	% Tarsus at 40 days
EC	1,074	44	57.1	70.8	1.1	87.5
EF	1,311	82	50.8	79.5	1.7	90.9
LC	1,069	130	84.8	67.9	2.6	92.4
LF	1,269	44	59.0	75.0	4.5	91.5

TABLE 4.   Parameters of two logistic regression models for the effects of hatch date, food supplementation, structural size (PC1) and body mass (both relative to group mean) on the probability of survival of captive-reared Greater Snow Goose goslings. Partial chi-squares reflect the independent contributions of the variables (see Methods for details).

Variable	B	Partial chi-square	df	P
a.) Effect of hatch date and food treatment on survival				
Hatch date	1.05	6.97	1	0.008
Treatment	0.27	0.93	1	0.33
Interaction	−0.27	0.35	1	0.55
Constant	0.74			
b.) Effect of relative body mass and size on survival				
Mass	9.01	4.43	1	0.035
Size	−7.39	1.21	1	0.27
Interaction	0.28	0.00	1	0.99
Constant	−0.81			

lighter ones, but larger goslings did not survive better than smaller goslings when mass was controlled for (Table 4b).

There were several proximal causes of mortality of goslings. Six goslings ceased to feed, became weak, and died. This includes one gosling of age 34 days that died following sexing by cloacal inspection several hours earlier. On two occasions, small goslings straggled from the main group of goslings. One was recovered dead, the other was not recovered and was presumed dead. Two goslings succumbed to apparent respiratory ailments, one was found dead in water, one died of exposure following a rain storm, and one died accidentally (the latter bird was excluded from the analysis on Table 4).

DISCUSSION

GROWTH

Because of mass-related death rates, our results on growth represent a conservative analysis of our treatment effects, being based on a subsample of heavier birds. Despite the conservative nature of our hypothesis test and the small age difference between early and late-hatched goslings (5–7 days), late-hatched goslings that survived had a lower mean growth rate and were smaller at 40 days than early-hatched ones. Supplementation of the natural diet with high quality food allowed late-hatched goslings to grow faster than unprovisioned early-hatched goslings. The difference in growth between early and late-hatched unprovisioned goslings can thus be attributed, to a large degree, to the difference in food supply. However, the effect of food supplements was not large enough to completely eliminate growth differences between early and late hatched goslings. The two groups of goslings with food supplements had equivalent diets (i.e., duck chow) for only half days, the rest of the time being spent foraging on natural vegetation with control goslings. As the quality of this portion of the diet was lower in late-hatched goslings than in early-hatched ones, this may have contributed to differences in growth related to hatch date in the two food-supplemented groups.

The steep decline in the quality of natural food during the summer at Bylot Island (Manseau and Gauthier 1993) is likely the most important factor in explaining the poor growth of late-hatched goslings. As the season progresses, fiber content in food plants increases whereas nitrogen concentration declines steadily. Nitrogen content of *Eriophorum* spp., the preferred food plant, is at its maximum (4.4%) about two weeks before the peak hatch date and declines by as much as 40% during the following five weeks (Manseau and Gauthier 1993). Although the nitrogen level may increase in plants after grazing (Cargill and Jefferies 1984), this effect is slight at moderate grazing levels and does not prevent the seasonal decline in food quality on Bylot Island (Gauthier, unpubl. data). Early-hatched goslings thus had access to food of higher quality than those hatched later. In herbivorous birds such as geese, the processing rate of materials in the digestive tract appears to limit the rate of food intake (Sedinger and Raveling 1988, Kenward and Sibly 1978). Therefore, we conclude that the decline in plant quality has an adverse effect on the growth of late-hatched goslings because they are unable to increase their food intake to maintain their nitrogen intake, a limiting factor for growth (Manseau and Gauthier 1993).

As the season progresses, plant biomass in preferred feeding sites decreases on Bylot Island due to grazing by geese (Gauthier, unpubl. data). Decline in food abundance as a result of heavy grazing has been linked to slow growth rates in Lesser Snow Geese (*C. c. caerulescens,* Cooch et al. 1993). In our experiment, however, grazing level was light as goslings were moved frequently between feeding sites, and wild geese avoided these sites because of the disturbance induced by our continuous presence (see METHODS). It is thus unlikely that late-hatched captive goslings experienced lower food abundance than early-hatched ones.

Other factors besides food may have contributed to differences in growth and survival between the four treatment groups. Late-hatched goslings experienced slightly lower temperature (mean minima: 4.0°C [late] vs. 4.7°C [early]) and more rain during their first three weeks than early-hatched goslings, conditions which may have increased their energy expenditure and possibly increased mortality. Annual reductions of growth rate in cold, wet years have been demonstrated in Lesser Snow Geese (Cooch et al. 1991b) and other precocial birds (e.g., Hunt and Hunt 1976, Jørgensen and Blix 1985). Early-hatched goslings were socially dominant over late-hatched ones but goslings were typically widely scattered on foraging sites and aggressive encounters were uncommon. Hence, competition between goslings

of different sizes was probably negligible. While they were in cages, the energy expenditure of food-supplemented goslings was possibly lower than that of control goslings because of reduced locomotory activity and shelter from wind. However, the absence of solar radiation would tend to have the opposite effect on energy expenditure of caged birds. Feeding time of unprovisioned goslings was also reduced compared to wild ones as they were outdoors for 19–20 hr each day instead of 24 hr as they would have been naturally. However, goslings did not lose potential foraging time to fleeing from predators, as wild goose families would. Finally, an alternative explanation to our results was that genetic differences between early and late-hatched goslings determined their growth and survival. Although we cannot rule out this hypothesis, Cooch et al. (1991a) provided good evidence that no systematic genetic differences in body size were associated with hatch date in Lesser Snow Geese.

One limitation of our experiment was that it did not continue until all goslings fledged. Growth data were therefore incomplete, particularly for late-hatched goslings. However, smaller goslings were unlikely to grow enough following the termination of the experiment to compensate for the size differences present before fledging. In Lesser Snow Geese and Barnacle Geese (*B. leucopsis*), smaller juveniles grew more after capture than larger geese when age was accounted for, but additional growth did not compensate for the differences already established (Cooch et al. 1991a, Larsson and Forslund 1991).

DEVELOPMENT OF PRIMARIES

In goslings without food supplements, development of the ninth primary started at a later age and a smaller body mass than in provisioned goslings. However, primary development began when the tarsus was about 90% grown regardless of treatment. Because goslings of low body mass are less likely to survive during migrations (Owen and Black 1989), Greater Snow Goose goslings in very poor condition may delay primary development to free resources for additional bone and muscle growth. However, such a strategy is risky as it decreases the likelihood of fledging before autumn freeze-up. Most of the fledging occurs less than 10 days before major departure of geese from Bylot Island for the southward migration (J.-F. Giroux and G. Gauthier, unpubl. data).

MORTALITY

Despite small sample sizes for survival analysis, our study shows that faster growth of goslings translated into higher survival to fledging. Mortality in late-hatched goslings was considerably higher than in goslings hatched only 5–7 days earlier, despite our care for sick goslings and protection against adverse weather. However, we found no direct evidence that supplementary feeding affected mortality. The lack of feeding effect is difficult to interpret but the power of our tests is low. The mortality relationships found in this study are unlikely to be limited to the period before fledging, because it is well known that the survival of juvenile waterfowl and other birds of low mass remains low after fledging (Owen and Black 1989, Haramis et al. 1986, Magrath 1991 and references therein).

TIMING OF NESTING

Our results are consistent with previous studies showing that growth rate decreases with advancing hatch date in birds (Perrins 1965, Cooch et al. 1991a, Sedinger and Flint 1991). We showed that, when potential differences in parental care were controlled for, access to high-quality food was the principal factor explaining the slower growth of late-hatched goslings. Limitation of nestling growth by food has been shown in many species that have temporally and spatially variable food supply such as insectivorous (Quinney et al. 1986, Stuart Simons and Martin 1990) or piscivorous birds (van Heezik and Davis 1990, Roby 1991). Even though goslings feed on plants, a less variable and more plentiful food supply, their growth also appears to be strongly food-limited, either because of its quality (this study, Larsson and Forslund 1991) or depletion through competition (Cooch et al. 1993).

Because of their short breeding season, arctic-breeding geese appear to be under strong selection pressure to lay as early as possible, because consequences for late-hatched young may include higher mortality, smaller size as a juvenile and adult (Cooch et al. 1991a, this study) and lower recruitment into the breeding population (Cooke et al. 1984). Yet, despite their northern breeding latitude, female Greater Snow Geese delay nesting by as much as two weeks following arrival on the breeding ground (Gauthier and Tardif 1991). Females, particularly young ones, may be unable to nest earlier because of the need

to acquire sufficient nutrients and energy to lay a clutch (Choinière 1992, Gauthier 1993). Earlier nesting may also lead to higher probabilities of nest failure by predation and desertion, as reported with female Lesser Snow Geese (Findlay and Cooke 1982). Balancing between the conflicting pressures of early hatching, nest predation, and nutrient acquisition during prelaying lead to highly synchronous hatching within the population. Nevertheless, we showed that a difference as small as 5 to 7 days in hatch date within a season has major fitness consequences.

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