

GROWTH AND ORGAN DEVELOPMENT IN GREATER SNOW GOOSE GOSLINGS

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ABSTRACT.—The tissue allocation hypothesis states that functional maturity and rapid embryonic growth are incompatible at the tissue level. This could explain why precocial birds, which have more mature tissues at hatching, grow more slowly than altricial birds. We evaluated this hypothesis in Greater Snow Geese (*Chen caerulescens atlantica*), which nest in the high arctic where the growing season is very short. We examined growth patterns and dry-matter content (an index of tissue maturation) of various tissues, and the accumulation of fat in 176 goslings collected from hatch on Bylot Island, Northwest Territories, to their staging area at Cap-Tourmente, Quebec (1 to 110 days). The mass-specific growth constant ($K = 0.093$) of goslings was among the highest of all precocial birds, including ducks. Goslings fledged at only 68% of adult mass, a low value compared with other species. The timing and rate of growth differed among tissues, indicating major shifts in the allocation of protein during growth. Growth rates for body mass, body ash, and total body protein were moderate. Leg muscles and digestive organs had an early and rapid growth rate. Breast muscles had one of the highest growth rates but started to grow very late. Fat accumulation began after fledging, forcing goslings to start southward migration with very little fat reserves. In early-growing tissues (digestive organs and leg muscles), water content was low at hatch, peaked before fledging, and decreased thereafter. This contrasts with the typical pattern in birds of peak values at hatch followed by a monotonic decline during growth. The high dry-matter content of tissues at hatch could be an adaptation to increase thermogenesis of goslings in cold water. A strong inverse relationship between exponential growth rate and functional maturity was found in breast muscles but was absent in early-maturing tissues. Ecological factors seem more important than embryonic constraints in explaining fast growth rates in geese. Received 26 February 1996, accepted 6 November 1996.

BIRDS HAVE VERY FAST GROWTH RATES, their young growing about twice as fast as mammals of equal size (Björnhag 1979). In his reviews of growth in birds, Ricklefs (1973, 1979a) noticed that the growth rate constant is inversely related to adult body mass and decreases with the precocity of the species. Birds that hatch with a larger proportion of mature tissues (i.e. precocial species) tend to grow more slowly than those that hatch in a more immature state (i.e. altricial species; Lightbody and Ankney 1984, Sedinger 1986). According to the tissue-allocation hypothesis, growth rate is inversely related to the degree of functional maturity because mature muscle function (i.e. capacity for thermogenic heat production), which requires differentiated tissues, is incompatible with embryonic growth, which requires undifferentiated tissues (Ricklefs 1979a). The size and degree of maturity of leg muscles in young birds are es-

pecially important in constraining growth rates because the leg muscles usually make up the largest skeletal muscle mass at hatching (Ricklefs 1979b).

In the Anatidae, growth rate varies considerably among species, although it generally is more rapid than in other precocial birds of similar size (Ricklefs 1973). High seasonal food availability and short breeding seasons, two characteristics of the environments used by anatids, are some factors explaining their rapid growth (Ricklefs 1973, 1983; Aubin et al. 1993). The largest anatids, geese (Anserinae), are precocial birds whose legs are proportionally larger than those of ducks, an adaptation to their more terrestrial lifestyle. Young geese have well-developed legs and are highly mobile at hatching. Yet, Björnhag (1979) found that geese have higher growth rates than several other precocial birds, including ducks. Aubin et al. (1986) also reported that Lesser Snow Geese (*Chen caerulescens caerulescens*) had a mass-specific growth constant almost as high as that of Common Terns (*Sterna hirundo*), a parentally fed precocial

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species with smaller legs than geese. Therefore, the fast growth rates of geese, in spite of their large, well-developed legs at hatching, appears to be a challenge to the tissue-allocation hypothesis.

Because most geese are long-distance migrants, newly fledged goslings also face the challenge of accumulating fat reserves for the southward migration at the same time as they are completing growth. The early onset of fall in the arctic imposes an overlap of these two energy-demanding processes. The problem of assimilating enough nutrients to meet these requirements is compounded by the declining quality of arctic food plants in late summer (Manseau and Gauthier 1993). Migration is a critical period for the survival of young geese, especially for those that do not complete their growth in time. In young Barnacle Geese (*Branta leucopsis*), mortality during migration between Svalbard and Scotland (4,000 km) is high and inversely related to body mass near fledging (Owen and Black 1989).

The objectives of this study are to examine the pattern of growth and maturation of various organs, and the process of fat accumulation in Greater Snow Goose (*Chen caerulescens atlantica*) goslings from hatching in the arctic until arrival at a temperate staging area, three months later. Greater Snow Geese are an interesting case because they are large geese that have one of the northernmost nesting areas and shortest brood-rearing seasons in North America (Owen 1980). This provided an opportunity to evaluate Ricklefs' (1979a) tissue-allocation hypothesis in a species breeding under extreme ecological conditions.

METHODS

Study area.—Greater Snow Goose goslings were collected in two different areas in summer and fall 1993. The first study area was located at the Bylot Island National Wildlife Refuge, Northwest Territories (73°08'N, 80°00'W). The site is the most important nesting colony of Greater Snow Geese (about 15% of the total population; Reed et al. 1992). The study area (50 km²) was in the lowlands of a glacial valley and is characterized by wet polygon tundra covered by a rich graminoid cover (see Gauthier et al. 1995). The growing period extends from early July to late August and the 24-h daylight period from early May to early August.

The second study area was located 3,000 km farther south at Cap-Tourmente, a National Wildlife Refuge

on the north shore of the St. Lawrence estuary (47°04'N, 70°47'W), 45 km downstream of Quebec City. Geese use two ecosystems on the refuge, the agriculture lands of the coastal plain and the tidal marsh dominated by American bulrush (*Scirpus americanus*). Cap-Tourmente is a major staging area for Greater Snow Geese coming from Bylot Island as well as those coming from other breeding colonies scattered across the Canadian arctic islands. The site is heavily used by geese from late September to early November. From the St. Lawrence estuary, geese migrate an additional 1,000 km to their wintering areas along the coast of the mid-Atlantic states (Gauthier et al. 1992).

Collecting methods.—We collected three goslings in as many nests during the hatching period on 5 and 6 July (median hatching date of 3 July in 1993; $n = 367$ nests). From 15 July to 6 August, we randomly shot 40 goslings from wild families (one per family) within 4 km of the base camp. From 9 to 14 August, four banding drives were carried out at four different sites within 8 km of the camp, just before the fledging period. In each capture, we sacrificed 24 goslings (12 males and 12 females). Within each sex, we randomly selected six early-hatched and six late-hatched goslings. Early and late-hatched goslings were defined as those >2 days or <2 days, respectively, than the median age of goslings caught in each banding drive (see below for aging method). Finally, on 22 August, we shot an additional seven goslings (all of them were flying, although their estimated ages showed that they tended to be late-hatched birds).

During the fall migration, we captured goslings with rocket nets at Cap-Tourmente. The rocket nets were installed in hayfields regularly used by geese. In three captures (5, 19 and 20 October), we sacrificed 10 randomly selected individuals (five of each sex) among the juveniles caught (42 to 45 juveniles were caught each time).

Birds were sexed by cloacal inspection. Morphometric measurements were taken according to Dzubin and Cooch (1992) shortly after collection by the same observer on all birds. Culmen, head, tarsus, and sternum lengths were measured with a caliper (± 0.1 mm). Lengths of the body, the 9th primary, and the longest tail feather (when feather tips had emerged from the sheath) were measured with a ruler (± 1 mm). Birds were weighed (± 1 g) with an electronic field balance.

Body composition analysis.—In feathered goslings, we removed feathers with a sheep shears and discarded them. The following tissues were removed and weighed immediately on an electronic balance (± 0.1 g): left breast muscles (pectoralis and supracoracoideus), left leg muscles (including all muscles originating along the femur or the tibiotarsus), esophagus (with proventriculus), gizzard, liver, and intestine. The length of the small intestine and caeca was measured (± 1 mm), and the contents of digestive tracts were removed, weighed, and subtracted from body mass. The carcass, with all previous organs

removed, also was weighed and then frozen. Frozen carcasses were passed through a meat grinder three times and a 100-g sample of the homogenate was retained. All tissues were then frozen in plastic bags until further analyses.

Water content was determined by freeze-drying tissues to constant mass. Dried tissues were then ground to powder. Fat was determined by weighing (± 0.0001 g) duplicate 1-g dried samples in cellulose thimbles and extracting them during 45 min in a Rafatec apparatus (Randall 1974) using petroleum ether as solvent. Extracting time was verified to ensure total fat recovery (see Gauthier et al. 1992). Total body fat was calculated by adding the amount of fat determined in all tissues. Abdominal fat was absent in goslings on Bylot Island but was present during the fall at Cap-Tourmente. When present, abdominal fat was also removed during the autopsy and its fresh mass added to total body fat because fat usually accounts for >97% of the mass of this tissue. Protein of muscles and viscera was estimated using the lean (i.e. fat-free) dry mass, and carcass protein using the ash-free lean dry mass because carbohydrate and ash are a negligible fraction of soft tissues (Drobney 1982). Total body protein and body water were the summation of protein and water content of all body tissues (excluding feathers that were discarded), respectively. Body ash (again, excluding feathers) was estimated by incinerating a 3-g sample of dried, homogenized carcass tissues in a muffle furnace at 550°C for 12 h.

Aging methods.—The exact age of collected birds was unknown (except for those collected at hatching) and therefore had to be estimated. Even though hatching is highly synchronous (87% of the 367 nests hatched over a 7-day period), aging birds by the difference in the number of days between collection date and the peak of hatching was too inaccurate in young birds. Indeed, we found a large variability in the development and size of individuals collected on the same date. We chose to use a multivariate index of body size to age goslings collected before the banding drives as recommended by Gilliland and Ankney (1992). We applied the principal component equation (PC1) developed by Lindholm et al. (1994) in captive goslings at Bylot Island in 1991 based on culmen, head, and tarsus length (all in mm). This equation was:

$$PC1 = 0.335 \text{ sculmen} + 0.335 \text{ shead} + 0.334 \text{ starsus}, \quad (1)$$

where

$$\text{sculmen} = (\text{culmen} - 29.61) / 10.39, \quad (2)$$

$$\text{shead} = (\text{head} - 68.01) / 18.40, \text{ and} \quad (3)$$

$$\text{starsus} = (\text{tarsus} - 53.17) / 17.67. \quad (4)$$

PC1 explained 99% of the variation in the original measurements (Lindholm et al. 1994). Age of individuals was then obtained from the curve of Lindholm et al. relating age and PC1 in captive goslings. The curve

for control, early-hatched young was used because it corresponded more closely to the growth of wild birds in the Lindholm et al. study.

Age of goslings collected during banding drives and shortly after fledging was estimated using the length of the 9th primary (mm). The relationship between age and 9th-primary length was established on a sample of known-age birds, i.e. goslings that were tagged in the nest at hatching and recaptured at banding in the same year. This was a more accurate method than the previous one because it was established on birds that experienced the same growth conditions as the birds that we collected. Because growth of the 9th primary is linear (Boyd and Maltby 1980, Lindholm et al. 1994), we estimated the age (days) of goslings captured in banding drives or shot after fledging by the following linear equation ($r^2 = 0.62$, $n = 102$, $P < 0.001$; SE of estimate 1.7 days):

$$\text{age} = 22.81 + (0.0991 \cdot 9\text{th-primary length}). \quad (5)$$

This method could not be used with the younger goslings collected during the summer because no known-age goslings were recaptured before the banding period.

Age of goslings caught at Cap-Tourmente in fall was estimated by the number of days elapsed between the median hatching date on Bylot Island (3 July) and the capture date. The use of other aging methods (i.e. 9th-primary length or body size) was not possible because growth of most body parts is completed by then. Even though the method based on median hatching date is less accurate, the relative error on age is small in 3-month-old goslings, which are almost fully grown. Although the use of different techniques to age birds may introduce some variability, it should not affect comparisons among various body components.

Data analysis.—The sigmoid growth curve of each tissue was modeled using the logistic equation (Ricklefs 1983):

$$M(t) = \frac{a}{1 + be^{(-Kt)}} \quad (6)$$

where a is the asymptote of the mass (g), b is the natural logarithm of the ratio of asymptotic to initial mass, K is a constant proportional to the rate of mass increase (growth rate), and t is age (days). These equations were calculated using a nonlinear least squares estimation technique.

The logistic equation generates fixed-shape curves, in contrast to more general growth models, such as the Richards equation, which allow shape to vary (Ricklefs 1983). The Richards equation introduces a 4th parameter, m , that controls the shape of the curve. When $m = 2$, the Richards equation is reduced to the logistic equation, whereas when m approaches 1, it is reduced to the Gompertz equation (Ricklefs 1983). When we applied the Richards model to our data, we found

TABLE 1. Parameters from logistic growth equations (see Methods) for body constituents and organs (lean dry mass; ash-free lean dry mass for carcass) in male ($n = 84$) and female ($n = 89$) Greater Snow Goose goslings. Adult masses are from the period of minimum body mass in the annual cycle (early March) outside the breeding season (Gauthier et al. 1992).

	<i>K</i>		<i>b</i>		<i>a</i>		Adult mass (g)	
	Males	Females	Males	Females	Males	Females	Males	Females
Body constituents								
Body mass	0.096	0.090	20.0	14.9	2,397	2,270	2,666	2,391
Body protein ^a	0.094	0.089	23.1	17.2	514	472	561	516
Body ash ^a	0.123	0.127	100.0	94.0	88.5	79.2	109 ^c	91.5 ^c
Body water ^a	0.124	0.117	31.7	21.7	1,400	1,312	—	—
Body organs								
Breast muscles ^b	0.263	0.275	1.31×10^5	1.87×10^5	52.6	50.4	64.4	57.8
Leg muscles ^b	0.174	0.173	93.5	62.4	23.9	22.2	25.7	21.1
Esophagus	0.138	0.161	16.1	15.2	4.9	4.5	—	—
Gizzard	0.338	0.285	83.2	43.1	32.0	29.9	34.3	34.0
Intestine	0.146	0.156	14.8	18.7	19.2	18.6	—	—
Liver	0.110	0.102	14.0	11.9	13.8	14.0	15.2 ^c	13.8 ^c
Carcass	0.102	0.096	34.0	23.8	363.0	328.7	—	—

^a Excluding body feathers.

^b Muscles from left side only.

^c Values from geese collected in April and May along the St. Lawrence estuary (G. Gauthier unpubl. data).

values of m close to, or higher than 2 (e.g. $m = 1.74$ for body mass). However, we did not retain the Richards equation in our final analyses because: (1) in several cases the nonlinear regression algorithm did not converge to a solution, a common problem when applying the Richards equation to variable data sets such as growth of individual organs (R. Ricklefs pers. comm.); (2) the improvement in the r^2 of the model was very low ($\leq 1.5\%$) compared with the logistic model; and (3) three-parameter equations simplify comparisons of growth curves among different organs and with other studies.

The proportion of dry matter in lean tissues was used as an index of the functional maturity of tissues (Ricklefs 1979b, Ricklefs et al. 1994). The relationship between the proportion of water in tissues and age was analyzed using polynomial regressions. We also examined the relationship between the exponential growth rate (the first derivative of the logistic equation) and the proportion of dry matter in lean tissues using linear regression (Ricklefs 1983, Ricklefs et al. 1994). The level of significance was set at $P < 0.05$ for all statistical tests.

RESULTS

The age of goslings collected between hatching and the banding period ranged from 1 to 34 days ($n = 43$). Goslings collected during banding drives were between 29 and 45 days of age ($n = 96$), and those collected at fledging were 39 to 46 days of age ($\bar{x} = 43$ days, $n = 7$) and capable of flying. Visual observations and track-

ing of six females fitted with satellite transmitters (J.-F. Giroux pers. comm.) indicated that departure of geese from Bylot Island for the fall migration occurred around 24 August 1993 (range 20 to 28 August), less than 10 days after the first goslings had been observed to fly (15 August). The first goose families were seen at the Cap-Tourmente staging area around 1 October (A. Reed pers. comm.), although arrivals occurred throughout most of October (pers. obs.). At Cap-Tourmente, the age of collected goslings ranged from 94 to 109 days ($n = 30$).

Sex differences.—Adult male Snow Geese are about 12% heavier than females. All body components of males are larger than females, with differences ranging from 10% in liver to 19% in body ash (Table 1). Although asymptotic values of growth equations were higher in males than in females for all body components except liver, sex differences were smaller in asymptotic values than in adults (e.g. 6% difference for body mass, 13% for body ash). Despite these differences, growth rates (as judged by K) of body components were similar between sexes (Table 1). Growth constants of body mass, body protein, body water, leg muscles, gizzard, and liver were slightly higher in males than females, whereas the reverse was true for body ash, breast muscles, esophagus, and intestine. Because of these small and inconsistent differences between sexes during growth, data from males

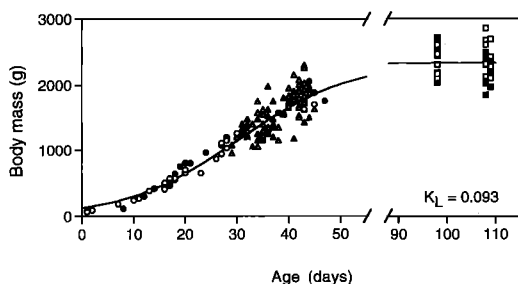


FIG. 1. Growth curve for body mass in Greater Snow Goose goslings. Open symbols = males; solid symbols = females; circles = goslings obtained by shooting; triangles = goslings caught in banding drives; squares = goslings caught in rocket nets. K_L = growth constant obtained from the logistic equation.

and females were pooled for the comparison of growth patterns among body components.

Body constituents.—Mean body mass of goslings increased from 80 g at hatching to 2,332 g in the St. Lawrence estuary, 110 days later (Fig. 1). Body protein had a growth pattern most similar to body mass (Fig. 2A), although it was slightly delayed (50% of asymptotic mass attained three days later; Table 2). The skeletal component (body ash) followed a similar growth pattern, although its growth was further delayed compared with body mass (50% of asymptotic mass attained seven days later; Table

TABLE 2. Timing of growth of body constituents and organs in Greater Snow Goose goslings. Fledging estimated at 43 days of age.

	% of asymptotic value at fledging	Age (days) at 50% of asymptotic value
Body constituents		
Body mass	76	30
Body protein	71	33
Body ash	69	37
Body water	87	27
Body organs		
Breast muscles	41	44
Leg muscles	95	19
Esophagus	97	18
Gizzard	100	13
Intestine	97	18
Liver	88	24
Carcass	76	34

2), and it eventually grew more rapidly (growth constant about 36% higher; Fig. 2A). Increase in body water was slightly ahead of body mass (50% growth attained three days earlier; Table 2) and was also faster (by about 30%). Growth of these constituents was not completed at fledging (43 days; proportion of asymptotic mass attained at fledging ranged from 69 to 87%; Table 2).

Fat was the constituent for which accumulation was most delayed. At hatching (0 to 2 days), vitellum accounted for at least 4% of the body mass and was composed of 85% of fat. This fat was rapidly catabolized by goslings soon after hatching, and during most of the growing period goslings were extremely lean (Fig. 3). Fat increased from $1.5 \pm$ SE of 0.2 g ($n = 9$) at 10 days of age (0.6% of total body mass) to $12.0 \pm$ 0.5 g ($n = 51$) around fledging at 40–45 days of age (0.7% of body mass). Accumulation of fat must be very rapid thereafter because goslings collected on the staging area 3,000 km farther south had 281 ± 15 g of fat ($n = 30$) at about 100 days of age (12% of body mass).

Organs.—The two locomotory muscle groups, leg and breast muscles, showed dramatically different timing and pattern of growth (Figs. 2 and 3). Leg muscles grew rapidly in the first days (50% of asymptotic mass reached 11 days before body mass; Table 2) and had almost completed their growth when goslings fledged around 43 days (Table 2). In contrast, breast muscles were the last organ analyzed to initiate growth, reaching only 50% of asymptotic mass near fledging. The asymptote estimated by the

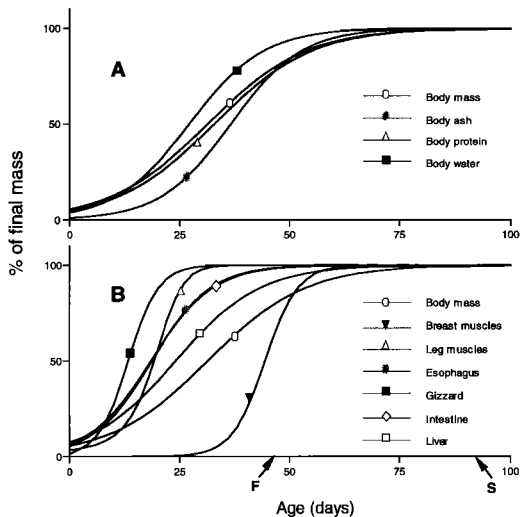


FIG. 2. Growth curves (% of asymptotic mass) for (A) body constituents and (B) organs (protein content) in Greater Snow Goose goslings. Body mass curves shown for reference. F = fledging age; S = age upon arrival at Cap-Tourmente staging area.

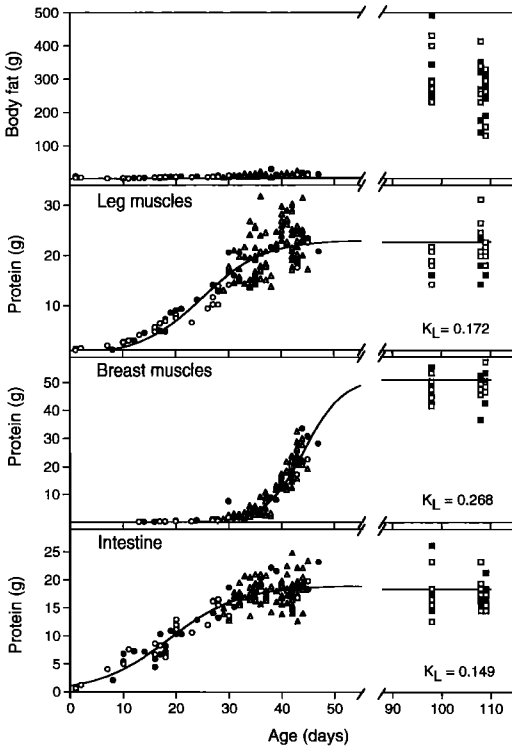


FIG. 3. Body fat and growth curves for protein content (lean dry mass) of leg muscles, breast muscles (left side only), and intestine of Greater Snow Goose goslings. Open symbols = males; solid symbols = females; circles = goslings obtained by shooting; triangles = goslings caught in banding drives; squares = goslings caught in rocket nets. K_L = growth constant obtained from the logistic equation.

growth curve was only 84% of adult size for breast muscles compared with 99% for leg muscles (Table 1), which suggests that significant growth of breast muscles continued after three months. Despite the late onset of its development, the growth constant for breast muscles ($K = 0.268$) was much higher than that for leg muscles ($K = 0.172$; Fig. 3), suggesting a very fast growth of the breast.

The growth of all digestive organs (esophagus, gizzard, intestine and liver) occurred early in the development of goslings (Fig. 2B). The development of the gizzard, which was the largest muscle at hatching, followed a trajectory similar to that of the legs and was extremely early and rapid. The gizzard was the earliest organ to develop (50% of asymptotic mass reached 17 days earlier than body mass) and had the highest growth constant ($K = 0.294$). Develop-

ment of the esophagus and intestine also occurred early (50% of asymptotic mass reached 12 days earlier than body mass; Table 2) and relatively rapidly ($K = 0.143$ and 0.149 , respectively; Fig. 3). The liver was the last digestive organ to develop although its growth was still relatively early (50% of asymptotic mass reached six days ahead of body mass; Table 2) and its growth moderate ($K = 0.104$). Because of their early development, these four organs had reached 88 to 100% of their asymptotic mass at fledging (Table 2). The remaining soft-body tissues (carcass) showed a growth pattern very similar to that for body protein (Tables 1 and 2).

Water content.—Water content differed both in absolute values and pattern of temporal variation among the various organs. The patterns of change in water content with age fell into two groups. In breast muscles and carcass, water content declined steadily throughout the growth period from peak values at hatching or shortly thereafter. In contrast, water content of leg muscles, gizzard, intestine, and total body increased during growth, peaked shortly before fledging, and declined thereafter as shown by the significant polynomial regressions (Fig. 4).

The largest change in water content occurred in the breast muscles, with values decreasing from an average of 82% soon after hatching to 71% at around 110 days of age (lean mass basis; Fig. 4). Water content also was relatively high at hatching, or soon after, in the carcass (75–78%), but declined to low values at 110 days (Fig. 4). Water content was lowest in the leg muscles (72%) and intestine (73%) at hatching but was relatively high at 110 days (75 and 77%, respectively) compared with the other organs (Fig. 4). Water content of the gizzard was especially variable in young goslings.

The tissue-allocation hypothesis predicts an inverse relationship between exponential growth rate and functional maturity of tissue. Using the proportion of dry matter in lean tissues as an index of maturity, we found no such relationship in leg muscles, gizzard, and intestine, all of which are organs that developed early (Fig. 5). In contrast, the prediction was upheld in breast muscles, carcass, and total body protein. However, for carcass and especially total body protein, several points were high above the predicted line. These were mostly goslings with both a high proportion of dry matter in their tissue and a high exponential growth rate, i.e. very young goslings (Figs. 4 and 5).

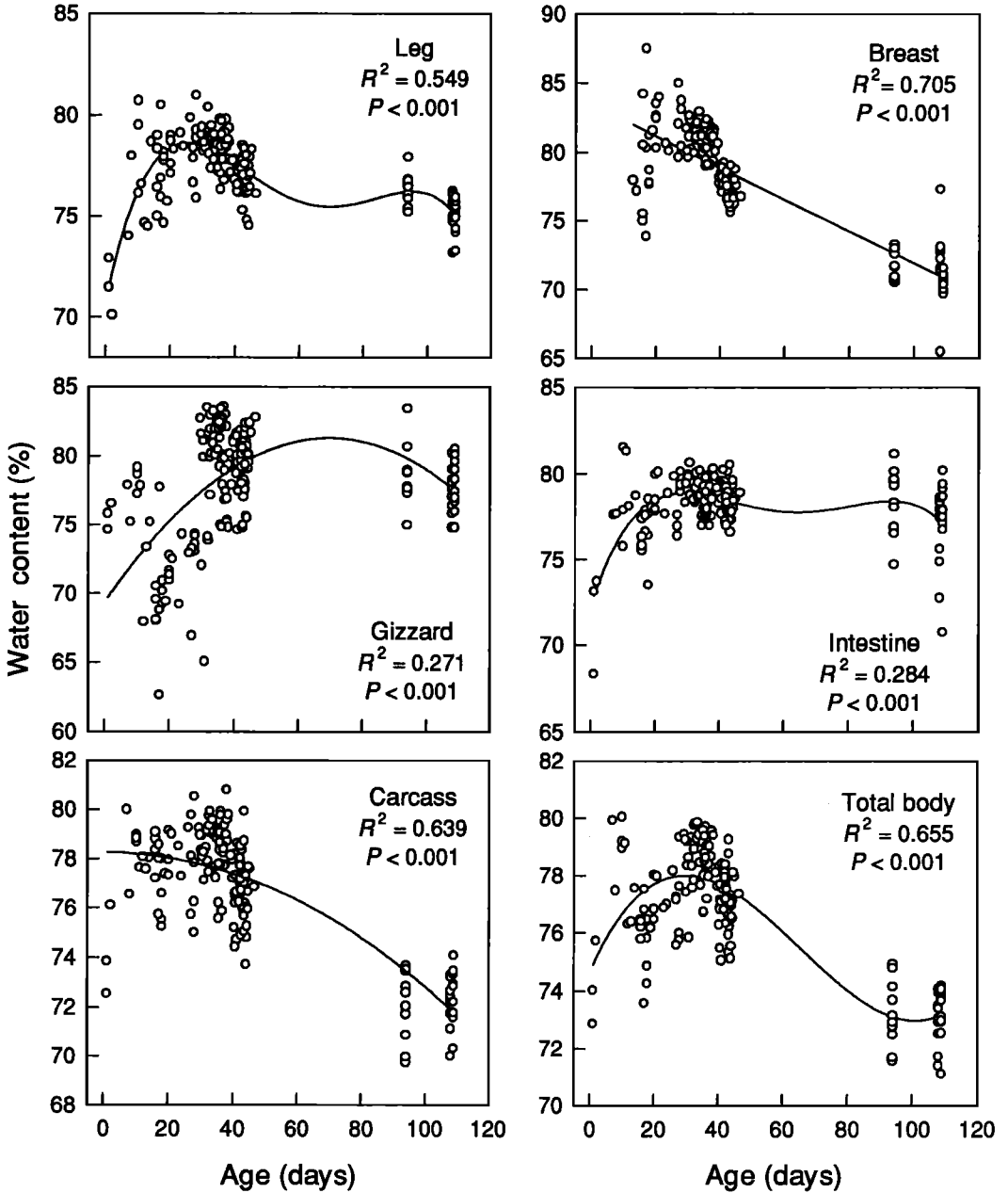


FIG. 4. Water content (water mass/lean mass; ash-free lean mass for carcass and total body) of leg muscles (left side only), gizzard, carcass, breast muscles, intestine, and total body of Greater Snow Goose goslings. Polynomial regressions (including only significant terms) are as follows: leg ($y = -1.15 \cdot 10^{-8} x^4 + 2.91 \cdot 10^{-6} x^3 - 2.48 \cdot 10^{-4} x^2 + 7.70 \cdot 10^{-3} x + 0.71$); gizzard ($y = -2.47 \cdot 10^{-5} x^2 + 3.44 \cdot 10^{-3} x + 0.69$); carcass ($y = -5.43 \cdot 10^{-6} x^2 + 0.78$); breast ($y = -1.16 \cdot 10^{-3} x + 0.83$); intestine ($y = -8.39 \cdot 10^{-9} x^4 + 2.08 \cdot 10^{-6} x^3 - 1.77 \cdot 10^{-4} x^2 + 5.85 \cdot 10^{-3} x + 0.72$); total body ($y = 2.77 \cdot 10^{-7} x^3 - 5.42 \cdot 10^{-5} x^2 + 2.49 \cdot 10^{-3} x + 0.75$). Water content (y) is expressed as a ratio, not a percentage, in the equations.

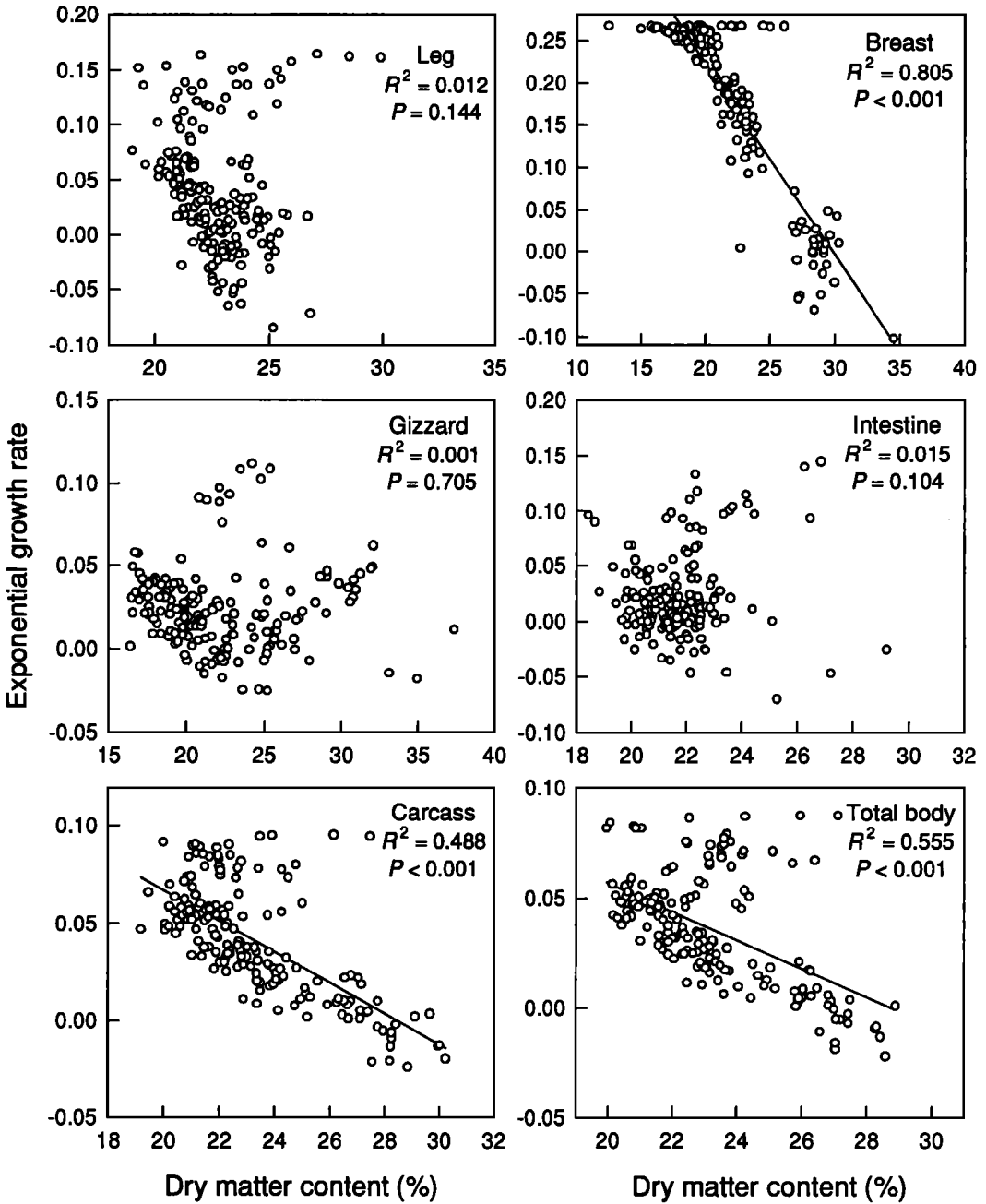


FIG. 5. Exponential growth rate (first derivative of logistic equation) plotted against dry matter content of lean tissues (100 - % of water; ash-free basis for carcass and total body), the latter an index of tissue maturity, in Greater Snow Goose Goslings. Significant linear regressions: carcass ($y = -0.793x + 0.226$); breast ($y = -0.354x + 0.283$); total body ($y = -0.646x + 0.186$).

DISCUSSION

Comparisons of growth rates among species are dependent upon the accurate estimation of growth parameters and the equations used. Growth equations are sensitive to the inclusion of fully grown young in the data set (Bradley et al. 1984, Sedinger 1992). Lack of data points near the asymptote may cause an underestimation of K and an overestimation of the asymptote value. When we applied the logistic equation to body mass data from 0 to 50 days of age, the estimated parameters ($K = 0.092$, $a = 2,350$; both sexes) were similar to those over the 110-day period (Table 1), with asymptotic values differing by less than 1%. However, when we used the Gompertz equation, an equation frequently used (Ricklefs 1983), the growth constant of Greater Snow Geese calculated over 0 to 50 days ($K = 0.045$) was underestimated compared with the 110-day period ($K = 0.062$), whereas the asymptotic mass was overestimated (0–50 days: $a = 3,099$; 0–110 days: $a = 2,362$). Because many studies fit growth curves only until fledging, some growth constant values may be biased downward when the Gompertz equation is used.

Patterns of growth.—Because growth rate is inversely related to body mass, allometric equations have been developed to allow interspecific comparisons. Ricklefs (1979a) described the relationship between K (for logistic growth) and M (asymptotic mass) in birds with the following equation: $K = 1.10M^{-0.34}$. Using an adult body mass of 2,525 g (minimum winter mass; Table 1), this yields a predicted K value of 0.077 for Greater Snow Geese. The K value that we obtained in goslings (0.093) is higher than the predicted value, which is surprising because the equation is largely based on altricial birds that should have faster growth rates than precocial birds like geese. When compared with precocial birds such as galliforms, geese also have a higher growth rate. For instance, if we scale the growth constant of Snow Geese to a bird the size of a quail (115 g; using the equation $K_2 = K_1 [M_2/M_1]^{-0.34}$), we obtain a K of 0.266 compared with 0.106 for Japanese Quail (*Coturnix coturnix japonica*; Ricklefs 1979b). This is in agreement with Ricklefs' tissue-allocation hypothesis, which states that birds with larger legs (the most mature muscles at hatching) should have slower growth rate (leg muscles account for 10% of body mass in Snow Geese at fledg-

ing compared with 17% in Japanese Quail; Ricklefs 1983).

However, this prediction no longer holds within the family Anatidae because Snow Geese, which have bigger legs than ducks (Sedinger 1986), generally grow faster than ducks. Sedinger (1992) estimated the relationship between adult body mass and growth constant (Gompertz equation) within the Anatidae as: $K = 0.31M^{-0.22}$. According to this equation, the predicted Gompertz K for a bird the size of a Greater Snow Goose (0.055) is indeed lower than the value that we obtained (0.062). Although the waterfowl equation may be biased downward by the inclusion of K values calculated on incomplete data sets (i.e. only until fledging; see above), this effect probably is counterbalanced by the inclusion of several studies on captive waterfowl that generally have faster growth than in wild birds (Sedinger 1992, Lindholm et al. 1994).

The growth constant for Greater Snow Geese is similar to that for Cackling Canada Geese (*Branta canadensis minima*; 0.072 vs. 0.074, respectively; Sedinger 1986) but lower than that for Lesser Snow Geese (0.100 vs 0.151; Aubin et al. 1986; in both comparisons, K for Greater was adjusted using $K_2 = K_1 [M_2/M_1]^{-0.22}$ to account for size differences). The discrepancy with Aubin et al.'s value is surprising although it is possible that his K values are overestimated because of the statistical technique used to calculate the growth equation in this study (Aubin et al. 1986).

Even though the growth rate of Greater Snow Geese appears similar to other, smaller geese, Greater Snow Geese fledge at the same age as Lesser Snow Geese (43 days), but five days younger than Cackling Geese. This is achieved by fledging at a lower percentage of adult mass; Greater Snow Geese fledge at 68% of adult body mass (1,853 g), whereas Lesser Snow Geese fledge at 79%, and Cackling Canada geese at 89% of adult mass (Sedinger 1986). The shorter summer period experienced by the Greater Snow Goose in its high breeding latitude may have favored fledging at an earlier stage of development than in the other species.

All these comparisons suggest that ecological factors could be more important than embryonic constraints in determining growth rates within the Anatidae. Selection for rapid growth is strong in arctic-nesting geese because the very short summer forces goslings to grow as quickly

as possible to reach fledging stage in time for the fall migration. Such a high growth rate in a herbivorous species is surprising. Indeed, geese are among the very few species of birds whose young rely entirely on plants to obtain all of the nutrients required for their growth (Aubin et al. 1993). Other herbivorous birds have a diet that includes animal food during growth because plants are poorer in protein than are animal tissues, and growth requires large amounts of protein (Sedinger 1992, Moss et al. 1993). However, the fast growth rate in geese is favored by the 24-h daylight of arctic regions during the summer, which allows for continuous feeding.

The growth constant we measured ($K = 0.093$) was lower than that of goslings raised under artificial conditions on Bylot Island, i.e. hand-reared, early hatched goslings with food supplement ($K = 0.168$; Lindholm et al. 1994). This difference further suggests that food availability limits growth rate in geese, either through a limitation in quality (Manseau and Gauthier 1993, Lindholm et al. 1994) or quantity (Gauthier et al. 1995).

Growth of individuals organs.—The growth of individual organs showed very contrasting patterns in Greater Snow Geese. Body organs can be divided in three groups according to their growth pattern (Fig 2). The first group, the supplying organs (Lilja 1981), is composed of leg muscles and digestive organs (esophagus, gizzard, intestine, and liver) that are characterized by an early and rapid growth soon after hatching. Investment in supplying organs is maximized early in development because goslings need mature legs in order to find food and mature digestive organs to process food efficiently. The rapid growth of the gizzard is especially impressive; between 8 and 16 days of age, 40% of all protein synthesized in the body is in this sole organ (estimated from Fig. 2). In addition to its essential digestive function, this organ also could play a role in thermogenesis of young goslings because it is the largest muscle at hatching (Sedinger 1986). The second group of organs to develop includes bones (body ash) and carcass (overall body protein), which are characterized by a moderate growth rate.

Finally, the breast muscles show a unique growth pattern. It is the last organ to develop but does so at a very fast rate, which concentrates the resource requirements for the development of these muscles in a short span of time. Indeed, from 40 to 54 days, more than 65% of

all protein synthesized in the body is in the breast muscles alone. Thus, growth of this large muscle mass monopolizes most of the resources devoted to growth by goslings around fledging time. Delaying development of these muscles until the end of growth allows goslings to maximize allocation of internal resources to the growth of large supplying organs such as the gizzard and legs at a younger age. In return, the very fast growth rate of breast muscles near fledging is possible because supplying organs have almost reached their adult size.

Growth rate and functional maturity.—According to the tissue-allocation hypothesis, functional maturity and rapid embryonic growth are incompatible at the tissue level (Ricklefs et al. 1994). The hypothesis predicts an inverse relationship between exponential growth rate and maturity at the tissue level. The proportion of dry matter in muscles is assumed to be a good index of maturity because it increases with the accumulation of contractile proteins and other functional elements as tissues mature (Ricklefs 1979b, Ricklefs et al. 1994).

A strong inverse relationship between exponential growth rate and maturity was only found in the breast muscles. The relationship also was present in the carcass and total body protein, but there was considerable variation in young goslings. In contrast, tissues that developed early and were most mature at hatching (leg muscles, gizzard, and intestine) showed no inverse relationship between growth rate and maturity. These tissues grew rapidly even though their water content was relatively low. These results again suggest that embryonic constraints are not the primary factor limiting growth rate in geese. However, constraint on growth at the organism level (Ricklefs 1979a) could be important in geese. There is evidence that nutrient intake in growing goslings is constrained by gut capacity (Sedinger and Raveling 1988, Manseau and Gauthier 1993, Piedboeuf 1996). When food quality declines, goslings are not able to process a larger quantity of food to maintain their nutrient intake, a common phenomenon in herbivores.

The increase in water content of several tissues from low values at hatching contrasts with the typical pattern in birds of a decline in water content from maximum values at hatching when tissues are least differentiated (Ricklefs 1979b, Ricklefs and White 1981). However, the pattern that we observed is not unique because other

studies also have reported an initial increase of water content in growing tissues of waterfowl (Clay et al. 1979, Aubin et al. 1986, Sedinger 1986). This could be a consequence of the precocial mode of development in anatids. In order to be functional at hatching, supplying organs must reach an advanced stage of maturation in the egg, which increases their dry matter content at hatching. However, this explanation is at odds with the fact that precocial galliforms such as quail generally have maximum water content values at hatching followed by the typical pattern of linear decline (Ricklefs 1979a).

As an alternative explanation, we propose that a much greater requirement for thermogenesis in newly hatched anatids compared with galliforms explains the high dry matter content of some their tissues at hatching. Unlike galliforms, anatids enter the water in the first hours after hatching. This increases their metabolic requirements considerably because in cold environments, the rate of heat loss is much faster in water than in air (Schmidt-Nielsen 1991). The capacity for thermogenesis is directly related to the dry matter content of tissues in newly hatched European Starlings (*Sturnus vulgaris*) and quail (Ricklefs and Webb 1985, Choi et al. 1993). Some results in waterfowl are consistent with this hypothesis. The metabolic scope (defined as the difference between peak and minimum $\dot{V}O_2$; Choi et al. 1993) is about 2.2 ml O_2 /g/h in newly hatched (1–3 days old) Greater Snow Geese (Ratté, LaRochelle, and Gauthier unpubl. data) and 2.8 ml O_2 /g/h in 1-day-old Common Eiders (*Somateria mollissima*; Steen et al. 1989), values twice as high as in newly hatched quail (1.2 ml O_2 /g/h; Choi et al. 1993). Visser and Ricklefs (1993) also reported much higher peak metabolic rates in the Anatidae compared with other precocial birds.

The requirement for high metabolic rate could have favored a high dry matter content in tissues at hatching while maintaining the potential for rapid growth. The subsequent increase in water content of organs during growth would occur because new relatively immature tissues would be added to these organs through cell proliferation. In contrast, water content peaks early in organs that are too immature at hatching to contribute to thermogenesis (e.g. breast muscles).

Fat dynamics.—As in other waterfowl species (Ankney 1980, Sedinger 1986), newly hatched Greater Snow Geese showed a rapid decline in

fat content of the body during the days following hatching. This corresponds to a transition period when yolk reserves are mobilized to sustain metabolism while goslings become competent in finding food (Clay et al. 1979). After this initial decline, the increase in fat content during growth was extremely slow, as observed in other goose species (Aubin et al. 1986, Sedinger 1986). Thus, the growth period was characterized by a very low level of fat (<1% of body mass). The absence of fat accumulation before fledging is surprising given the early onset of migration in this species (i.e. shortly after fledging). It appears that all ingested nutrients largely were allocated to protein production rather than to fat accumulation at fledging.

By the time geese arrived at the Cap-Tourmente staging area, 4 to 5 weeks after leaving Bylot Island, goslings had accumulated large amounts of fat. Although some fat may be stored in the few days following fledging, this suggests that goslings leaving Bylot Island for migration (ca. 10 days after fledging) cannot fly long distances. Goslings will need to stop frequently, at least in the first part of the migration, to accumulate fat stores, and this should impose a slow rhythm of migration on their parents (family groups migrate together). This could explain the long fall migration (4 to 5 weeks) of Greater Snow Geese in contrast with the short spring migration (<1 week; Gauthier and Tardif 1991). Goslings must therefore have access to high-quality feeding areas during migration in order to gather enough energy and nutrients to complete the growth of some tissues (e.g. breast muscles), cover the cost of migration, and arrive on the fall staging area with a surplus of fat. The small fat stores of goslings at the onset of migration probably reduce their ability to cope with harsh environmental conditions encountered during migration, such as bad weather and poor food availability, and may increase their mortality.

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