GROWTH OF LESSER SNOW GEESE ON ARCTIC BREEDING GROUNDS[1]

A. E. AUBIN

Gravenhurst High School, P.O. Box 370, Gravenhurst, ON P0C 1G0, Canada

E. H. DUNN AND C. D. MACINNES[2]

Ontario Ministry of Natural Resources, Wildlife Research Section, Maple, ON L0J 1E0, Canada

Abstract. Wild Snow Geese (*Chen caerulescens*) at the McConnell River, Northwest Territories, Canada, grew rapidly for their size, requiring only 30 days to grow from 10 to 90% of asymptotic weight (1,475 g). Fledging occurred at about 72% of adult weight. Culmen and tarsus were close to adult size at fledging, but primaries were only 65% grown. Fat and water indices resembled those of altricial birds. Captive geese differed in growth patterns from wild birds, particularly in feather and tarsal growth and in water index, but showed the same pattern of caloric density. Snow Geese and other anatids grow more rapidly than other precocial species and do not appear to support Ricklefs' hypothesis concerning the inverse relationship between growth rate and proportion of functionally mature tissue at hatch.

Key words: Lesser Snow Goose; growth rates; anatids; body composition.

INTRODUCTION

Despite much recent research on Lesser Snow Geese (*Chen c. caerulescens*), we know of no published data on the development of wild goslings. The few data for growth of geese of any species are primarily for captives (Roberson and Francis 1965, Yocum and Harris 1966, Morehouse 1974, Würdinger 1975, Ankney 1980). Such growth rates, however, can differ markedly from those of wild goslings (e.g., Würdinger 1975). We report here on growth of wild Snow Geese at the McConnell River, Northwest Territories, Canada (60°50′N, 94°25′W), giving comparative data from semicaptive goslings raised at the same site.

METHODS

Four thousand wild goslings were marked at hatching in 1971 with individually numbered web tags. Growth was studied in web-tagged goslings which were reencountered either when captured in mass banding drives or when shot from towers located on the feeding grounds. Data from only the first encounter were used, to avoid statistical problems of repeated measures from the same individual, and because growth may be slowed for a few days after recapture (A. Dzubin, pers. comm.). Data were also collected from a few non-web-tagged goslings, whose ages were estimated from eye lens weight. The following measurements were taken: culmen—the exposed culmen, measured with vernier calipers to the nearest 0.1 mm;

tarsus—from the epiphysis to the distal end of the tarsometatarsus, measured with vernier calipers to the nearest 0.1 mm; primaries—numbered 1 through 10 (proximal to distal), measured unflattened from tip to point of insertion to the nearest 1.0 mm with a ruler; body weight—weighed on spring scales, with birds <1 kg weighed to the nearest 1.0 g, and those heavier weighed to the nearest 10.0 g.

Additional information was taken from collected birds: Gizzard—opened and cleaned organ was weighed on a top-loading electric balance to 0.1 g; intestine—portion extending from the gizzard to the cloaca was cleaned and weighed to 0.1 g; eye lens—whole eyeballs were removed from all collected birds and stored in 10% formalin for 2 to 4 months, then lenses were removed and dried in an oven at 75°C for 24 to 40 hr.

All collected birds were weighed and were measured externally. After removal of gizzard contents, the birds were chopped into smaller pieces and ground in a meat grinder until homogenization was complete. Ground birds were frozen and analyzed further after the field season, all within a few months.

A subsample (usually at least 100 ml, and comprising at least 10% of the homogenate) was freeze-dried to determine water content. On average, 9% of live weight was lost during storage, and this was assumed to be water. Lipid was extracted from at least two, and usually three or four aliquots of the dried sample (about 0.5 g each), using the Goldfisch method with petroleum ether as the solvent. Live weight caloric content was estimated by converting tissue composition to calories (9.00 kcal/g fat and 4.78 kcal/g lean dry; Ricklefs 1974). Oxygen-bomb calorimetry on about half the sam-
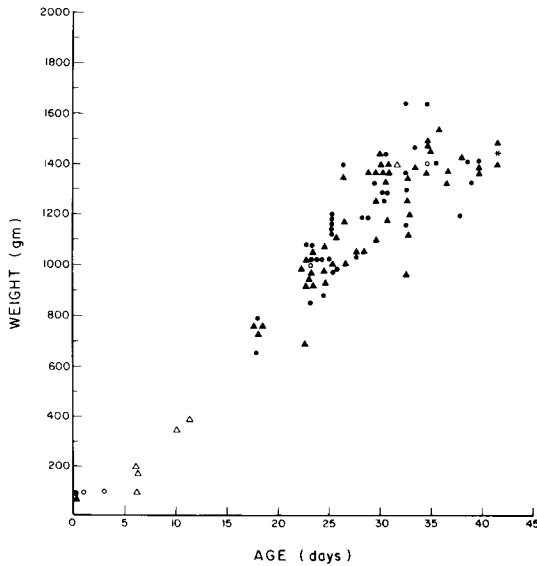
FIGURE 1.   Weights of individual wild Snow Goose goslings. Circles indicate males, triangles females, and asterisks unknown sex. Open symbols show birds whose age was estimated from eye lens weight. Values for hatchlings are means for 9 males and 9 females.

ples gave a value of 4.93 kcal/g lean dry ($n = 42$). The micro-Kjeldahl method was used to measure nitrogen content (Schmidt 1961). The same methods were used in analyzing yolk from 68 fresh eggs and 9 yolk sacs removed from hours-old hatchlings.

Thirty-five goslings taken from nests during hatching were held for a week in cardboard cartons placed near an oil burner. Dog food and water were supplied freely. After a week, the goslings were placed in a 0.6-ha enclosure made of 95-cm high poultry fence with 2.5-cm mesh, placed around a traditional goose feeding area. Although the goslings fed mainly on vegetation, largely *Carex* spp., they were provided with a supplement of dog food (Miracle brand, minimum 25% protein), given at the rate of 0.09 g per g of goose per day. Water was freely available from a stream flowing through the area. All birds were measured twice a week as described above. A sample of these (usually four) was collected weekly for other analyses (see above).

Equations describing weight and measurements of wild birds during growth were determined by fitting polynomials with linear regression (SPSS Statistical Package), allowing stepwise entry (after inclusion of age) of age^2, age^3 and a dummy variable for sex. This method does not impose a curve of any particular form onto the data and offers a readily obtained, statistically meaningful indication of the effect of sex. Weight data were further fit to a logistic curve (SAS NLIN program) to obtain standard parameters (K, t_{10-90}) for com-

parison to results of other growth studies (Ricklefs 1983). The log of each side of the equation was taken, to equalize residuals at each end of the growth curve and to reduce the effect of extreme values on estimation of the asymptote.

Comparison of captive bird growth to that of wild birds was made by fitting polynomials to data for both groups combined, as above, but including a dummy variable for captivity status. Because repeated measurements were taken on captives, data were included only for those birds with at least 12 measures taken over at least 35 days (6 males and 6 females). Data for captive goslings were weighted (weight = 1/total cases for that bird) to give each individual equal representation, whether wild or captive. The equations given in this paper were fit to data for wild birds alone.

RESULTS

Snow Geese developed rapidly, with scapulars first showing at 10 to 12 days and primaries at 18 days. Most fledging in 1971 took place only 10 days before the start of migration. A logistic curve fit to weights of wild goslings (Fig. 1) gave a t_{10-90} (days between 10% and 90% of asymptotic weight, 1478 g) of 30 days and a K (growth rate constant) of 0.151. The sexes did not differ in the course of weight gain ($P > 0.05$), although adult males outweighed adult females, and just-hatched males weighed more than females (83.4 g for 9 males vs. 77.4 g for 9 females, t-test $P < 0.01$).

The equation for culmen on age in wild birds (Fig. 2A) was $Y_{mm} = 17.542 + 0.862$ age $- 0.0001$ age^3 ($r^2 = 0.98$, SE of regression = 1.58, $n = 112$). Average length of primaries 1 to 10 of wild goslings (Fig. 2C) was linear with respect to age ($Y_{mm} = -149.419 + 6.993$ age; SE = 7.60, $n = 70$). The equation for eye lens growth (Fig. 2D) was $Y_{mg} = 36.130 + 1.577$ age $+ 0.120$ age$^2 - 0.002$ age^3 ($r^2 = 0.98$, SE = 7.33, $n = 63$). Sexes differed only in tarsus length (Fig. 2B, $P < 0.05$), with males growing faster ($Y_{mm} = 30.126 + 2.063$ age $- 0.001$ age^3 for females, $Y_{mm} = 31.892 + 2.063$ age $- 0.001$ age^3 for males ($r^2 = 0.98$, SE = 2.82, $n = 114$). Sexes are combined in Figure 2B because of the smallness of difference between them.

Growth of the gizzard and intestine in wild birds was examined relative to overall body growth. A regression of log organ weight on log body weight shows whether organ growth is relatively more rapid (slope of regression, $b > 1.0$) or slower ($b < 1.0$; Ricklefs 1983). Gizzards grew rapidly in the first week after hatching ($b = 1.31$), then more slowly ($b = 0.89$ for days 8 to 35). After 35 days, actual gizzard weight appeared to decrease (Fig. 3A).
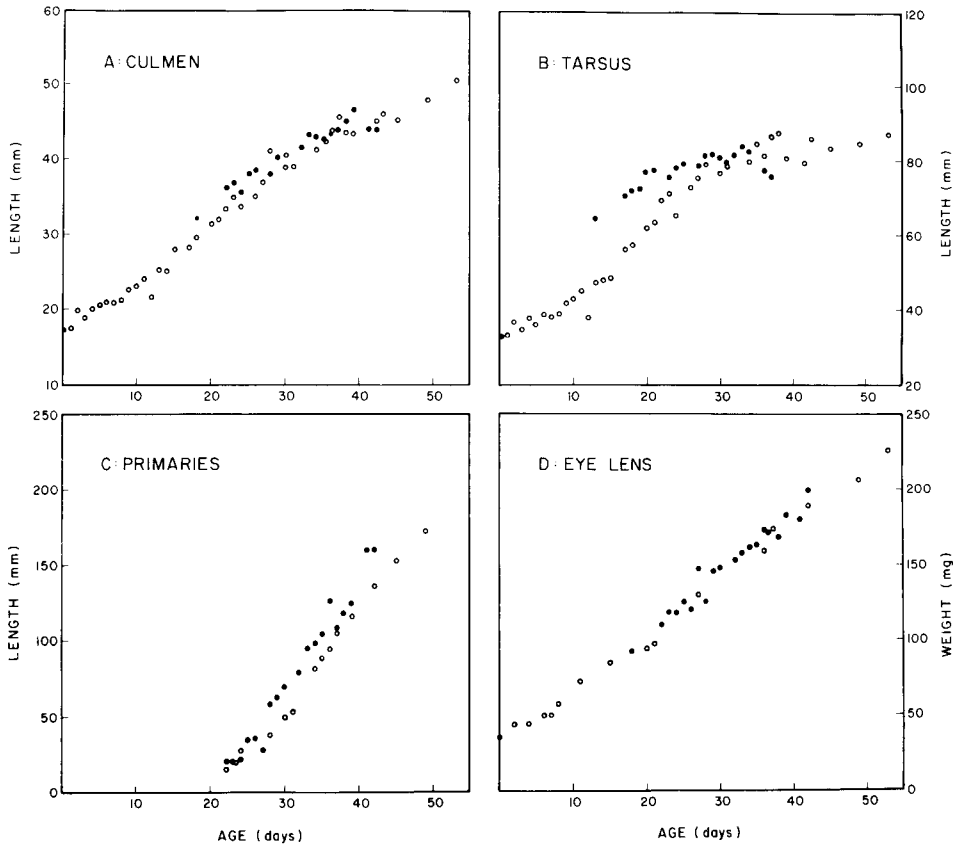
FIGURE 2. Mean culmen (2A), tarsus (2B), primary length (2C), and eye lens weights (2D) of known age goslings, sexes combined. Values for primaries are average length of Primaries 1 to 10. Solid symbols = wild goslings; open symbols = captives.

Growth of the intestine (Fig. 3B) resembled that of the gizzard (b under 8 days was 1.45, and 0.85 from 8 to 35 days).

Water index (Fig. 4A) decreased linearly after the first week. Lipid indices were extremely low (Fig. 4B), except at hatch when yolk sacs ranged from 5 to 15% of fresh body weight. Even without yolk sacs, the lipid index for hatchlings was high. This reflected extra body fat reserves that were, like the yolk sac, used up within a few days. Caloric content of the live bird increased linearly from 0.8 to 1.8 kcal/g from time of yolk sac absorption to fledging (Fig. 5). Water and fat index and caloric density were not affected by sex ($P <$ 0.05).

Nitrogen content was measured to see if it would provide a good index of physical condition, as it is related to the amount of protein in the body. Multiple regression showed that log nitrogen content was directly proportional to log lean dry weight ($n = 42$, $r^2 = 0.68$, $b =$ 0.94, $P < 0.001$), with no additional effects of age, sex, feather length, or log fat content. It therefore provided no more information on condition than did less-tediously obtained values such as weight.
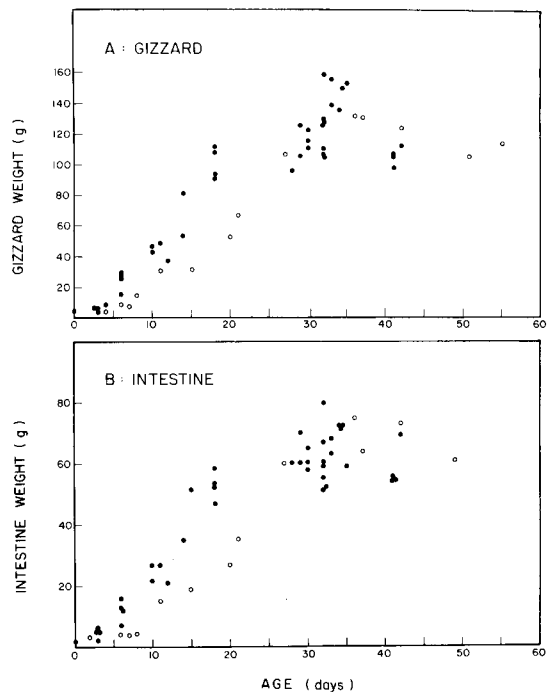
FIGURE 3. Gizzard (3A) and intestine weight (3B) of individual wild goslings (sexes combined, solid symbols). Means for captive birds at each age are shown for comparison (open symbols).
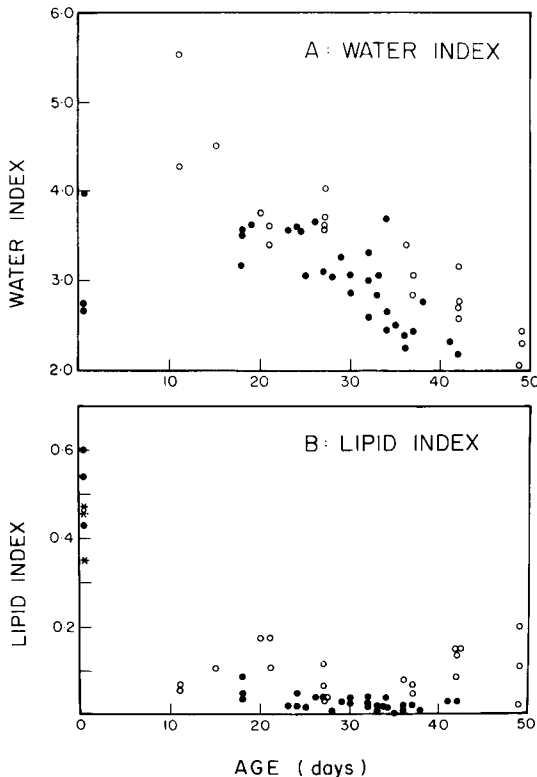
FIGURE 4. Water (4A) and lipid (4B) indices of individual known-age goslings (sexes combined). Index is water or lipid content divided by lean dry weight. Solid symbols = wild goslings; open symbols = captives. Asterisks denote lipid indices of hatchlings with yolk sac removed.

FIGURE 5. Live weight caloric content of individual known age goslings, calculated from composition (see Methods). Symbols as in Figure 4.

Growth of captive goslings was the same as for wild birds only in weight gain (to the age of fledging) and in eye lens growth (see Methods). Captives continued to gain weight after the age of fledging (42 days), and it is assumed that wild birds did also. Culmen, tarsus, intestine, and gizzard growth lagged significantly in captives for the first month (Figs. 2 and 3), but reached final sizes similar to those of wild goslings. In captive birds, the decrease in gizzard weight late in growth was clearer. Primary growth of captives (Fig. 3C) lagged consistently behind that of wild birds.

Captive birds had higher water content than wild birds (Fig. 4A, $P < 0.05$), but the rate of dehydration (excluding hatchlings) did not differ. Lipid indices were higher ($P < 0.05$) after the first week (Fig. 4B), perhaps as a result of the supplemented diet. Caloric density, however, was the same in captives as in wild goslings (Fig. 5).

Composition of eggs and yolk sacs were investigated (Table 1) to determine whether rapid development in wild Snow Geese might result from particularly large energy reserves at hatching. Yolk was larger in larger eggs ($P < 0.001$, $b = 0.313$, $r^2 = 0.24$), as found by Ank-

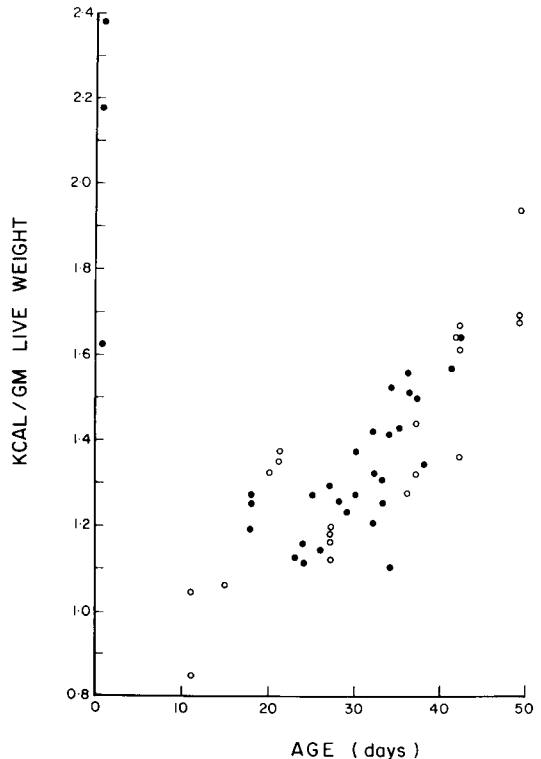ney (1980), and other results are summarized in Table 1.

DISCUSSION

Weight gain of wild Snow Geese was as rapid as for altricial species of the same size (Fig. 6). However, data were not available after the age of fledging. Because many anatids gain more weight after fledging and all other growth curves for anatids but one were fit to data from captives that could be measured beyond the age of fledging (Ricklefs 1973), t_{10-90} for Snow Geese may have been underestimated. Nearly all other precocial species were also studied in captivity (Ricklefs 1973), however, and it should be safe to conclude from Figure 6 that anatids grow more rapidly than other precocial birds.

By the age of fledging, Snow Goose body weight was about 70 to 75% of that of adults, and primaries were about 65% grown (Table 2). These proportions are at the low extreme of the ranges given in Owen (1980) for several goose species (75 to 96% and 70 to 85%, respectively).

Canvasback (*Aythya valisineria*) and Lesser Scaup (*A. affinis*) showed patterns of gizzard and intestine growth similar to those of the Snow Goose (Lightbody and Ankney 1984). A decrease in gizzard weight in Red-throated Bee-

TABLE 1. Composition and energy in fresh egg yolks and hatchling yolk sacs of Snow Geese. Sample sizes are in parentheses.

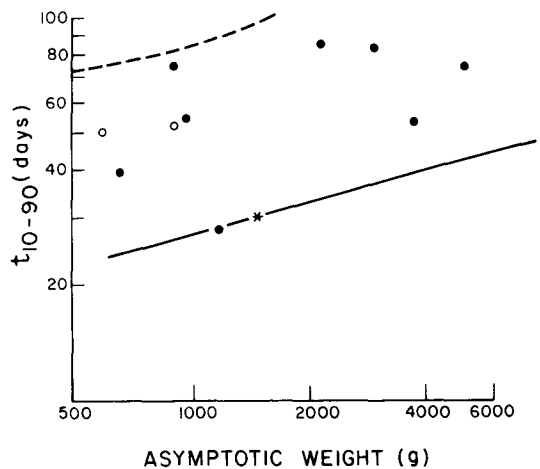|	Egg yolk	Yolk sac
Fresh egg or hatchling wt. (g)	124.3 (68)	80.9 (10)
Yolk or yolk sac wt. (g)	47.0 (68)	8.3 (10)
Yolk or yolk sac as % egg or hatchling wt.	37.8	10.2
% water of fresh wt.	47.1 (68)	48.0 (11)
% lipid	29.5 (6)	25.3 (11)
kcal/g fresh wt.	4.06	3.80

FIGURE 6. Days between 10% and 90% of weight gain from hatch to asymptotic weight in anatids. Solid regression line is for altricial species and dashed line for other precocial birds (Tetraonidae, Phasianidae, Meleagridae and Rallidae; Ricklefs 1973). Solid symbols for data from Ricklefs (1973), open symbols from Lightbody and Ankney (1984), and asterisk for Snow Goose (this paper).

eaters (*Merops bulocki*) has been attributed to a switch in food source late in growth (Fry 1972), but this cannot be the explanation in waterfowl. Decreases in internal organ weights late in growth may instead facilitate fledging. Gizzard and intestine development in waterfowl are more similar to those of seven altricial species than to those of the few semiprecocial and precocial species studied, e.g., Herring Gull *Larus argentatus* and domestic fowl *Gallus gallus* (Dunn 1975), in that digestive organs in the latter grow more slowly than the body as a whole throughout the post-hatch period.

If water index of wild goslings in the first 10 days after hatching is close to that of captive ones (Fig. 4A), then Snow Geese adhere to the pattern seen in Wood Duck *Aix sponsa* (Clay et al. 1979) and Herring Gull (O'Connor 1984). In these, water index first increases after hatch, instead of decreasing steadily throughout growth as is typical of other precocial species.

Although high body fat at hatching has been found in other precocial species (Ricklefs 1974), the low lipid level seen in wild Snow Geese later on (Fig. 4B) is unusual. Indices reached values of 0.30 and higher in some species (Brisbin and Talley 1973, Clay et al. 1979), but may have been artifacts of those birds being raised in captivity on an artificial diet. Alternatively, the low lipid storage in Snow Geese could reflect high allocation of energy to growth in an environment in which food (grasses and sedges) is in relatively uniform supply throughout de-

velopment. The values for live weight caloric density of wild Snow Geese (Fig. 5) are very similar to those of altricial species (Dunn 1975), mainly because of low lipid accumulation.

Caloric value for fresh egg yolk (Table 1) was similar to those for three domestic galliform species, but lower than in domestic waterfowl (4.39 kcal/g in domestic duck and goose, Ricklefs 1974). Hatchling yolk sacs averaged 11.4% of yolk-free body weight; within the range found both in galliform and anseriform species (10 to 25%, Ricklefs 1974). Thus, rapid growth of goslings did not appear to be connected to qualities of the egg.

Except for the eye lens, measurements of captive birds differed enough from those of wild birds that they could not be used to predict ages of wild goslings. In our captives, early growth tended to lag behind that of wild birds, but some conditions of captivity can produce unusually rapid development. For example, captive Snow Geese raised at the McConnell

TABLE 2. Size of wild Snow Goose goslings at fledging (taken as 42 days) with respect to adult size. Gosling data from equations fit to data in Figures 1 and 2 (see text). Sample sizes for adults in parentheses.

Age	Sex	Weight (g)	Culmen (mm)	Tarsus (mm)	Primary (mm)[a]
Fledgling	M	1,475	46	81	144
	F	1,475	46	80	144
Adult[b]	M	2,186 (207)	57.3 (35)	83.9 (35)	235 (20)
	F	1,912 (243)	55.4 (49)	79.9 (49)	223 (38)
Fledgling as % of adult	M	67	80	97	61
	F	77	83	100	65

[a] Average length of Primaries 1 to 10.
[b] Data for McConnell River adults in late summer 1970 (Lieff 1973; MacInnes, unpubl.).

River by Ankney (1980) reached weights at fledging (42 days) averaging 750 g more than our wild goslings at the same age, and 170 g more than adults (Table 2); tarsus lengths were 2.5 mm larger than in adults. Retardation of feather growth in captives (Fig. 2C) appears to be common, having been casually reported for geese (Hanson and Jones 1968) and well-documented in Ring-necked Pheasants *Phasianus colchicus* (Etter et al. 1970).

Ricklefs (1979a, 1983) hypothesized that a high proportion of maturely functioning tissue at hatch should lead to slow growth. In species studied to date, the parts of the body that function early (particularly the legs in precocial and semiprecocial species) grow more slowly than the rest of the body. Because overall growth rate should depend most on growth of body parts composing a large proportion of total mass (e.g., legs), Ricklefs (1979b) suggested an inverse correlation of growth rate with the relative size of legs in adults. Legs (including bones) make up 16.5% of adult Japanese Quail (*Coturnix japonica*), which grow slowly, but only 4.5% of adults in the fast-growing Common Tern (*Sterna hirundo*). Ducks, with legs making up 5 to 9% of adult body weight, have intermediate growth rates (Ricklefs 1979b, Fig. 6). Geese are terrestrial and cursorial and should have proportionately larger leg mass than ducks. In Cackling Geese (*Branta canadensis*), leg muscle alone constitutes 7 to 14% of adult weight, depending on season (Raveling 1979). Assuming proportional leg size of Snow Geese is similar to that of Cackling Geese, Ricklefs' hypothesis would predict an intermediate to slow growth rate for the Snow Goose. When the growth rate of Snow Geese (0.151) is scaled to the body size of quail and terns, however ($K_2 = K_1(W_2/W_1)^{-0.28}$, Ricklefs 1979b), it is as high (at 0.300) as that of the tern. Growth patterns of geese could still support Ricklefs' hypothesis if a large proportion of leg growth is completed before hatch, but goslings are so small relative to adults that this seems unlikely. Geese should be studied more closely with the objective of investigating Ricklefs' ideas.

ACKNOWLEDGMENTS

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