GROWTH AND DEVELOPMENT OF CANADA GOOSE GOSLINGS[1]

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Abstract. Under natural conditions goslings of Cackling Canada Geese (*Branta canadensis minima*) grew more rapidly ($k = 0.074$, Gompertz equation) than ducks but at a rate similar to other arctic nesting geese. Lipid levels in 2-day-old goslings were sufficient to meet energy requirements for less than one additional day. The liver, legs, and components of the gastrointestinal tract in Cackling Geese were relatively larger at hatching than in altricial birds. These tissues completed growth about three weeks before fledging as compared to one week in similar sized altricial birds. Early growth of digestive organs is probably related to the herbaceous diet of geese. Comparison of growth patterns of gallinaceous birds with those of geese superficially supports Ricklefs' hypothesis that proportion of mature tissue at hatching regulates growth rates. Examination of growth within the Anatidae, however, suggests that temporal patterns in food quality and availability may have been important influences in the evolution of growth patterns in these species.

INTRODUCTION

Growth patterns of young birds determine nutritional requirements and the length of the pre-fledging period. Lack (1968) concluded that growth rates in birds represent a compromise between faster growth, which reduces losses to predators, and slower growth, which allows adults to feed more young (in altricial species). In precocial species slower growth should better enable young to feed themselves. Ricklefs (1968, 1973, 1979) argued that available evidence does not support Lack's hypothesis, and he proposed that birds grow as fast as possible, given physiological constraints on tissue growth, i.e., tissues that are relatively mature at hatch tend to slow growth rates because the rate of cell division declines as tissue matures (Ricklefs and Weremiuk 1977). Thus, birds hatched with a larger percentage of mature tissue (precocial species) tend to grow more slowly than those hatched in a relatively immature state (altricial species). Recently, Ricklefs (1984) reexamined Lack's hypothesis and concluded that it reasonably explained variation in growth rates of altricial birds, but that physiological limitations might still play a role in the lower growth rates of precocial birds.

Waterfowl are precocial, but their growth rates are intermediate between those of some other precocial (galliforms) and altricial species of birds (Ricklefs 1973). Several studies have described growth patterns of waterfowl species but only those by Reinecke (1979), Braithwaite

(1981), Sugden et al. (1981), and Lightbody and Ankney (1984) calculated growth rates by fitting data to growth curves; only Dzubin (1959), Wurdinger (1975), Reinecke (1979), and Braithwaite (1981) described growth under natural conditions.

Growth patterns of geese are of particular interest because geese are almost strictly herbivorous (Owen; 1980, Sedinger and Raveling 1984), and most species nest in arctic areas with short growing seasons. As a result, relatively nutritious foods are available for a short period during the breeding season (Sedinger and Raveling, unpubl.). This could favor the evolution of faster growth patterns in arctic nesting geese to better synchronize the period of most rapid growth with the availability of high quality foods. I examined growth patterns in Cackling Canada Geese (*Branta canadensis minima*) under primarily natural conditions in order to examine Ricklefs' hypothesis in view of waterfowl growth patterns and to consider how the growth patterns of geese are related to the phenology of their foods.

METHODS

MAINTENANCE AND COLLECTION OF GOSLINGS

Cackling Geese nest in coastal tundra on the Yukon-Kuskokwim Delta, Alaska. Goslings were removed from nests located around Old Chevak (a U.S. Fish and Wildlife Service field station, 61°N, 165°W) and the Onumtuk Study Area (see Mickelson 1975 for a description of the area) during hatching and placed in fenced enclosures (ca. 3-m radius) for the first eight and five days after hatching in 1978 and 1979, respectively. The pens contained sedges and grasses typical of tundra meadow vegetation in the area (see Mickelson 1975, Sedinger and Raveling 1984 for details of vegetation). This procedure facilitated imprinting of the goslings

on the investigator. In 1978 I kept the goslings inside a cabin between 2400 and 0600 for their first six days to simulate brooding; I extended the period of overnight "brooding" to ten days in 1979 owing to predation on imprinted goslings by Glaucous Gulls (*Larus hyperboreus*). Following release from the enclosure, goslings ranged freely on an area used by Cackling Geese for rearing broods. The diet of imprinted goslings was augmented with poultry starter (24% protein, 5% lipid, 3% fiber) during their first ten days, primarily during the overnight period (less than 100 g per gosling for the 10-day period) during both 1978 and 1979. This allowed imprinted goslings to feed while inside during hours when wild goslings fed (i.e., between 0400 and 0600 and sometimes between 2400 and 0100).

Imprinted goslings were sacrificed by thoracic compression or cervical dislocation, and wild goslings were collected either by the same techniques or by shooting. Specimens were frozen within 24 hr following collection and were kept frozen until processed.

DISSECTION AND CARCASS ANALYSIS

I dissected and analyzed carcasses as described by Raveling (1979) except for slight differences noted below. Briefly, the procedure involved shaving contour feathers with sheep shears and plucking down feathers. The gizzard, liver, one half of the breast muscles (pectoralis, supracoracoideus, and coracobrachialis), and the muscles of the right leg were removed and weighed (wet) to the nearest 0.1 g on an Ohaus triple-beam balance. The lengths of the small intestine and ceca (both sides plus the diameter, when flattened, of intestine in between) were measured to the nearest millimeter following removal from the carcass. Contents of the gastrointestinal tract were removed and weighed. The entire carcass (except the liver and breast muscle) was homogenized by passing it through a commercial meat grinder three times using 5-mm openings in the grinder plate. The liver, half breast muscle, and two aliquots (ca. 20 g in the smallest goslings, up to 40 g in larger birds) of the carcass were analyzed in the following manner: water and lipid were determined by freeze-drying samples to constant weight (7 days) followed by extraction with ethyl ether (7 days) and oven drying at 100°C to constant weight (12 hr). Ash content was measured by burning samples in a muffle furnace at 600°C for 12 hr. Protein was estimated to be the lipid and ash-free dry weight which excluded protein in feathers. Carbohydrate was ignored because it comprises less than one percent of total carcass weight (Klei-

ber 1975). Sex of goslings was determined by gonadal examination.

AGE OF GOSLINGS

I estimated the age of wild goslings to be the number of days from the peak of hatching (21 and 20 June in 1978 and 1979, respectively) to the date of collection. Hatching was highly synchronous, with 70% and 83% of clutches in 1978 and 1979, respectively, hatching between 18 and 27 June (Sedinger and Raveling, in press). Thus, errors in estimated ages of wild goslings were most likely less than five days. One exception to this methodology was a brood of four (three males and one female) collected on 27 June 1979, which were known to have hatched about 48 hr earlier and were classified as two days old. Tame goslings in 1978 hatched on 18, 19, and 21 June. Unfortunately, six of these goslings lost their individual marks. As a result, ages of imprinted goslings were known to within one day for those sacrificed when younger than 17 days or older than 37 days, while ages of other imprinted goslings in 1978 were estimated by assuming they hatched on 20 June. Ages of imprinted goslings were known to within one day in 1979.

CURVE FITTING AND STATISTICAL ANALYSIS

Using the BMDP derivative-free, nonlinear least-squares curve fitting routine (Dixon and Brown, 1979), I fitted growth curves to data for weights of the total body, leg muscle, liver, gizzard, and carcass protein, and for lengths of ceca and small intestine. Growth patterns of these carcass components were modeled by the Gompertz equation (Ricklefs 1968) of the following form:

$$W(t) = A \cdot \exp(-b \cdot \exp(-kt)),$$

where A is the asymptotic weight, b is the *ln* of the ratio of asymptotic to initial weight and k is a constant proportional to growth rate. Growth data for the same carcass components were also fitted to a reparameterized version of the Richards' equation:

$$W(t) = [A^{(1-m)} - (A^{(1-m)} - B^{(1-m)}) \exp(-(1-m)kt)]^{1/(1-m)},$$

in which k was replaced by:

$$\frac{2(m+1)}{T(1-m)},$$

(Brisbin et al., in press). A and B correspond to asymptotic and initial weights, respectively, while k is proportional to growth rate and m is a shape parameter. The growth rate constants (k) in the Gompertz and Richards equations are not strictly comparable. I used the integrated form of the Richards' model rather

than the process-error form because each data point represented a separate individual; hence, data were not autocorrelated (see White and Brisbin 1980, for a discussion of various forms of the Richards' model and problems associated with autocorrelation of data). Total carcass lipid was fitted by linear regression because variability in the data obscured nonlinear patterns, and there was no indication that the rate of lipid deposition declined at fledging. I also fitted breast muscle data using linear regression after transforming age to ln (49.1 − Age) because these data did not converge to a solution using the Gompertz or Richards' models.

I examined differences between the growth curves of goslings from 1978 and 1979, and between imprinted and wild goslings using the following F test:

$$F = \frac{(SS_1 - SS_2)/(df_1 - df_2)}{SS_2/df_2},$$

where SS_1 is the sum of squares from a fit to the combined data for the two treatments and SS_2 is the sum of the sums of squares of fits to the data from each treatment group separately (White and Brisbin 1980). The same test was used to compare fits to the two growth models with SS_1 resulting from the fit to the three-parameter Gompertz equation and SS_2 from the fit to the four-parameter Richards' curve. Comparisons between treatments whose data were fitted to linear regression models were made using analysis of covariance.

RESULTS

The Richards' and Gompertz curves were fitted to 13 and 14 sets (18 possible, 2 sexes × 9 carcass components) of carcass component data respectively. I did not fit total carcass lipid data to this model (see above) and BMDP would not converge to solutions for breast muscle (both models) or female ceca length data (Richards' model). The Richards' model provided a significantly better fit than the Gompertz model only for male liver weights ($F_{1,21} = 7.18$, $P < 0.05$). Because of the lack of difference between the two models, I restricted further analysis to the Gompertz model because it fit data from other waterfowl studies well (Sugden et al. 1981, Lightbody and Ankney 1984) and because it allowed comparison to a greater number of studies. Parameter estimates from analysis using the Richards' model are presented in the Appendix.

Fitting data from imprinted and wild goslings separately, to either linear regression models (total lipid and breast muscle) or to the Gompertz equation (other components) resulted in five differences (F-tests, $P < 0.05$)
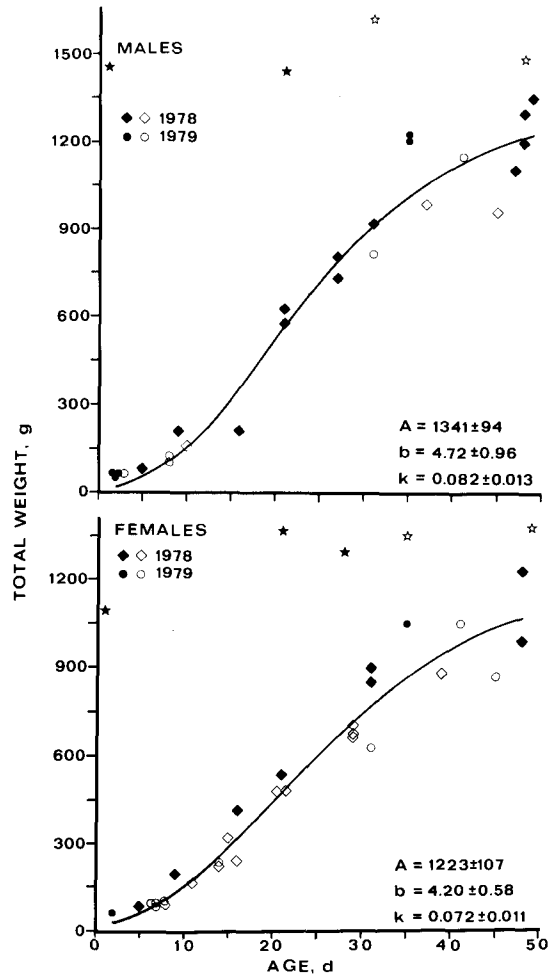

FIGURE 1. Weights (minus ingesta) of Cackling Goose goslings. Solid symbols represent wild goslings; open symbols represent imprinted goslings (see Methods). Stars represent values for adults. Solid stars are from Raveling (1979); open stars are from this study. Adult data are plotted to correspond to gosling ages on the dates adults were collected, assuming goslings had hatched at the peak of hatch. Parameter estimates (±SE) and solid curves are the result of fitting all data within each sex to the Gompertz equation (see Methods).

from 18 comparisons. However, imprinted and wild goslings differed for both sexes only when fitting data for small-intestine length. Differences between imprinted and wild goslings were not consistent between the sexes for two of the three components in which there was a significant difference for one sex (e.g., the estimated asymptote of liver weight was larger for imprinted than wild females, but larger for wild than imprinted males). Furthermore, standard errors of parameter estimates for imprinted and wild goslings overlapped for components in which there was a difference between the two groups. Because of the small number of significant differences between imprinted and wild goslings and the inconsistent pattern of
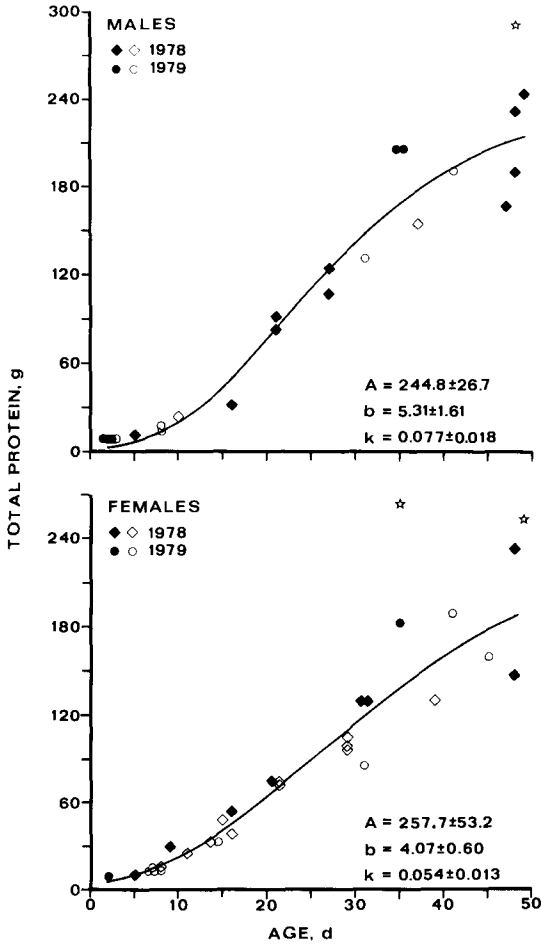
FIGURE 2. Total protein content of Cackling Goose goslings. Symbols as in Figure 1.
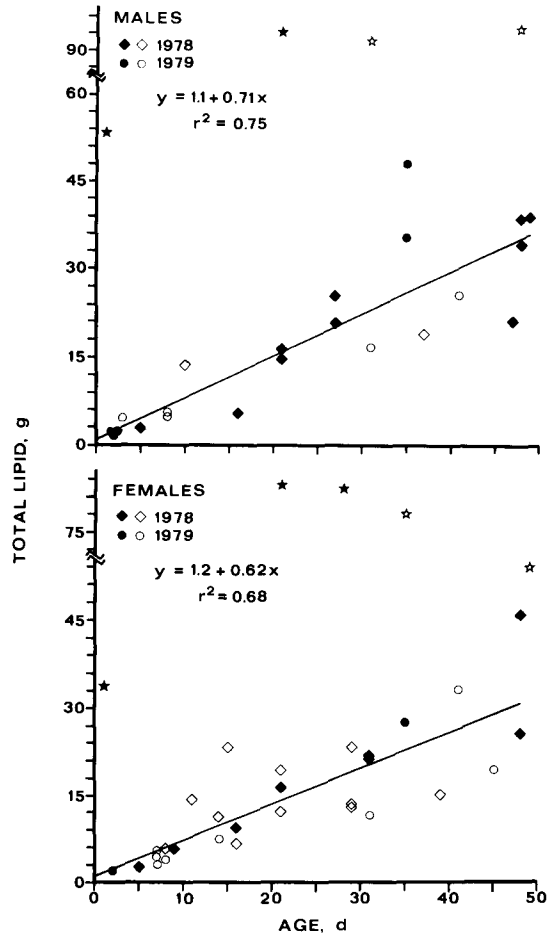
FIGURE 3. Total lipid content of Cackling Goose goslings. Parameter estimates and solid lines are the result of performing linear regression on all data within each sex. Symbols as in Figure 1.

differences, I pooled data from imprinted and wild goslings in subsequent analyses.

Comparison of goslings from 1978 and 1979 using the same method as for imprinted vs. wild goslings resulted in only two differences (leg muscle and liver weights of males) from 18 analyses. I pooled data from goslings collected in 1978 and 1979 because so few differences existed between these two groups.

WHOLE BODY GROWTH

Growth of Cackling Goose goslings (Fig. 1) was well described by the Gompertz equation with growth rate constants (k) of 0.082 and 0.072 for males and females, respectively. Male goslings (three collected at 48 and 49 days in 1978) and female goslings (largest female collected at 48 days in 1978) fledged at 87% and 89%, respectively, of concurrent adult weights. Total carcass protein (Fig. 2) and lipid (Fig. 3) were both increasing at fledging although the rate of protein deposition had declined.

MUSCLE AND VISCERA DEVELOPMENT

Leg muscles gained weight rapidly until goslings were between 30 and 35 days old (Fig. 4). For goslings more than 34 days old, leg muscle weights were 72% and 71% of concurrent adult levels for males and females, respectively. Breast muscles began to grow at a substantial rate when goslings were about 15 days old (Fig. 5), with the most rapid increase near fledging (after 40 days of age). Fledged goslings had breast muscles between 62% (males) and 74% (females) of adult values. Lipid content (percent of dry weight) of gosling breast muscles was maximum (50 to 60%) up to 10 to 15 days following hatching (Fig. 6) and declined thereafter. Lipid concentrations reached constant levels of about 9% of breast muscle dry weight at 35 days of age. The breast-muscle water index (water [g] divided by lean dry weight [g], Ricklefs 1979), while quite variable in young goslings, declined from 4.4 at 27
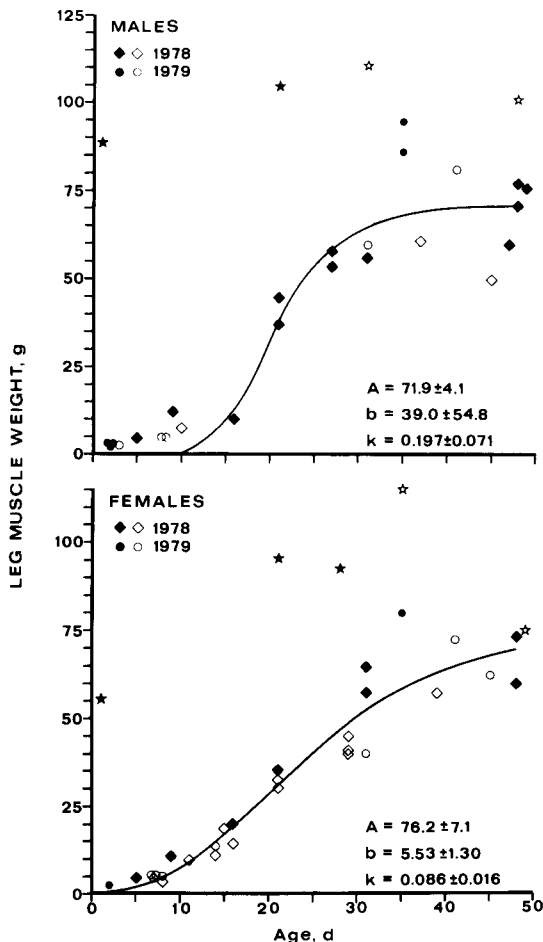
FIGURE 4. Weights (wet) of leg muscles of Cackling Goose goslings. Symbols as in Figure 1.

to 31 days of age to 3.2 at 48 to 49 days of age (Fig. 7), which was equal to adult values at that time.

Liver weights reached adult levels when goslings were about 30 days old and remained essentially constant until fledging (Fig. 8). Livers contained maximum lipid concentrations (37 to 55% of dry weight) at hatching (Fig. 9). Liver lipid concentrations declined rapidly following hatching, reaching a constant level (16% of dry weight) at about 15 days of age. Gizzards reached adult weight when goslings were about 35 days old (Fig. 10), while both the small intestine (Fig. 11) and ceca (Fig. 12) reached adult length at gosling ages of between 25 and 30 days.

The gizzard was the largest muscle weighed at hatching (11 to 12% of body weight), while leg muscles and breast muscles comprised 4% and 0.5% of body weight, respectively (Table 1). Leg and breast muscles each comprised an increasing fraction of total body weight, while livers and gizzards constituted decreasing fractions of total body weight as age increased.
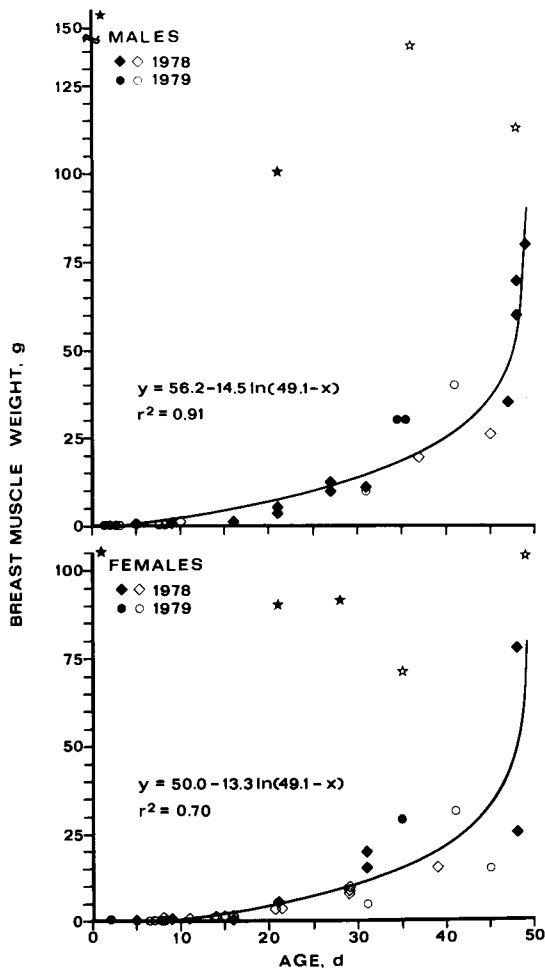

FIGURE 5. Weights of breast muscles of Cackling Goose goslings. Parameter estimates and solid lines are the result of performing linear regression on all data within each sex. Gosling ages were transformed to ln (49.1 − Age) to linearize the data prior to regression analysis. Symbols as in Figure 1.

DISCUSSION

STATISTICAL AND EXPERIMENTAL PROCEDURES

Uncertainty about the ages of wild goslings undoubtedly contributed some variability to the analyses presented here. While this variability was partially responsible for the sizes of standard deviations of growth curve parameter estimates, it should not have systematically biased my results. I attempted to use tarsus lengths to estimate ages of goslings of unknown hatch date. Besides the circularity inherent in such estimates, they were unsatisfactory for goslings older than 30 days because the relationship of tarsus length and age began to reach an asymptote at that age.

I believe that variability in age estimates also accounted for differences (nonsignificant)
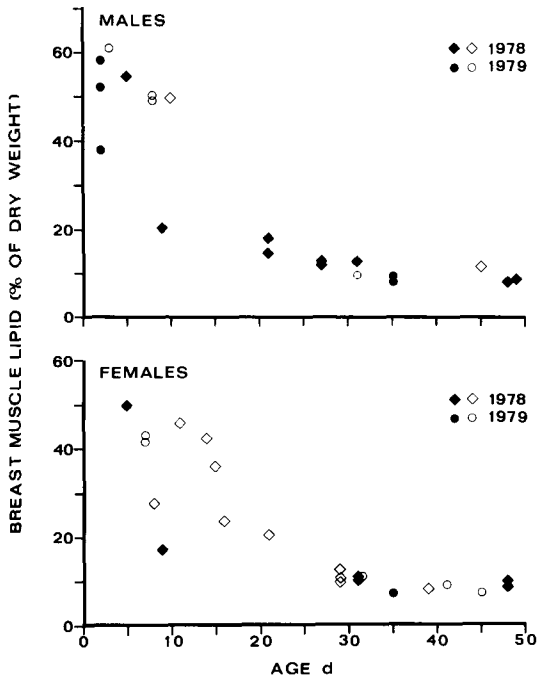
FIGURE 6.   Lipid content (percent of dry weight) of the breast muscles of Cackling Goose goslings. Symbols as in Figure 1.
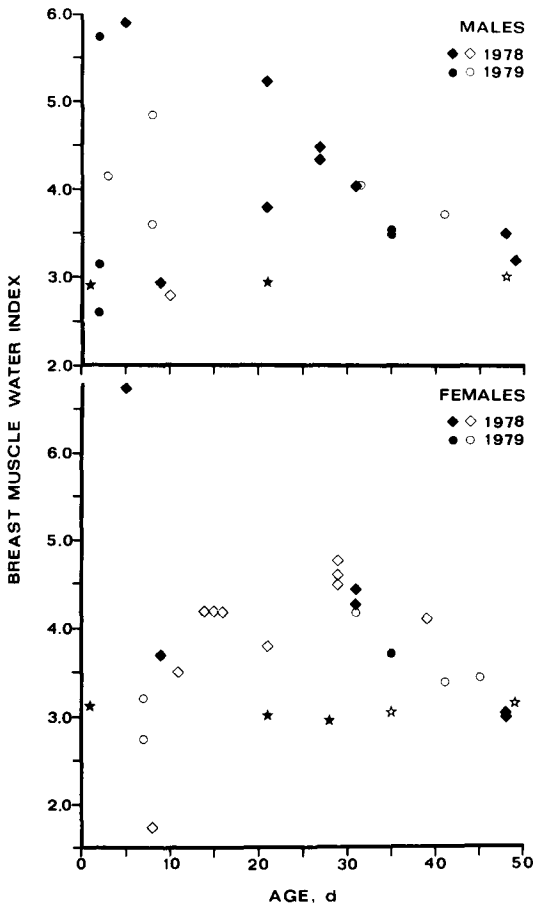
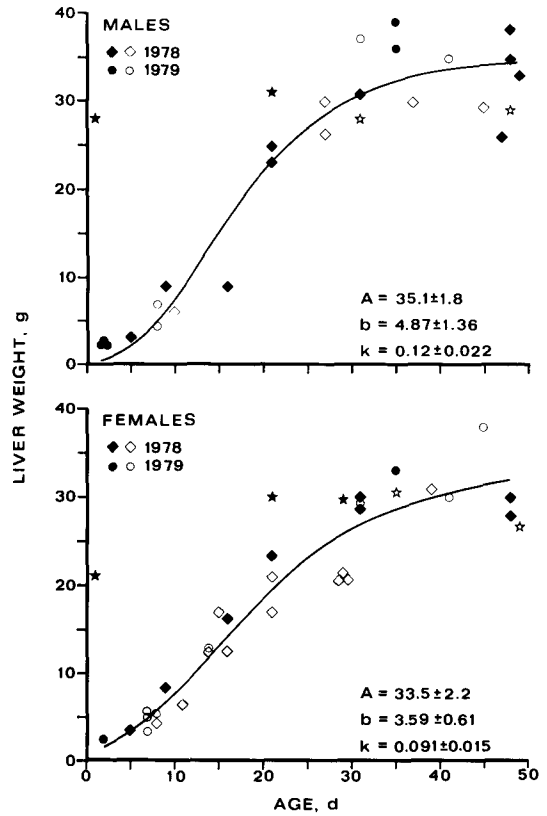FIGURE 7.   Breast muscle water index for Cackling Goose goslings. Symbols as in Figure 1.

FIGURE 8.   Weights (wet) of livers of Cackling Goose goslings. Symbols as in Figure 1.

between sexes, which presumably fledged at the same age and hence should have had similar k values. The growth rate for the sexes combined was 0.074, which was similar to growth rates for other arctic nesting geese (see below). A further problem with fitting curves to data for total body weight is that waterfowl generally do not reach a "true" asymptote in weight at fledging (Dzubin 1959, Kear 1970, Lightbody and Ankney 1984), as indicated by gosling weights lower at fledging than those of adults at the same time. However, I believe that most of gosling weight gain after fledging and before the next spring was lipid because lipid content of the carcass was still increasing steadily at fledging (Fig. 3) and weights of juvenile Cackling Geese in California, following fall migration, were similar to those of fledglings (add 48 g to fledgling weights in Table 1 to account for ingesta and compare to Raveling 1978a), indicating that most weight gained after fledging was lost during migration. Thus, I feel that declines in rates of increase for total body weight reflected a leveling-off in the increase of lean body weight at fledging, but the weight of carcass lipid probably increased up to the time of fall migration. However, goslings must have gained lean body weight at some
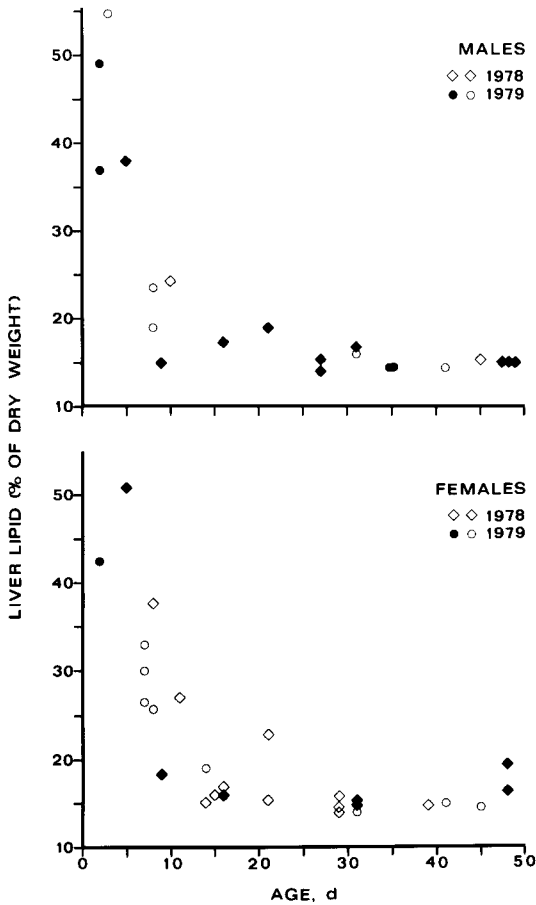
FIGURE 9.   Lipid content (percent of dry weight) of livers of Cackling Goose goslings. Symbols as in Figure 1.

FIGURE 10.   Weights (wet) of gizzards (empty) of Cackling Goose goslings. Symbols as in Figure 1.

time following fledging and prior to reaching reproductive age, because fledging weights were lower than those reported for adults in spring by Raveling (1979).

Regression models used to describe increases in lipid and breast muscle weight only apply to goslings through the fledging period. Rate of lipid deposition may have changed following fledging because Cackling Geese began to consume more energy-rich seeds and berries near fledging (Sedinger and Raveling 1984). The model describing growth of breast muscle approaches infinity at fledging age. While this equation cannot represent growth beyond fledging, it can model growth that is initially slow and later rapid.

Finally, the numerical methods used to estimate parameters of growth curves may not converge to the best fit to the data when estimates of parameters are highly correlated with each other (Davies and Ku 1977). This is the probable explanation for the unusual parameter estimates (particularly b and k) for the growth curves of the legs of male goslings (Fig. 4).
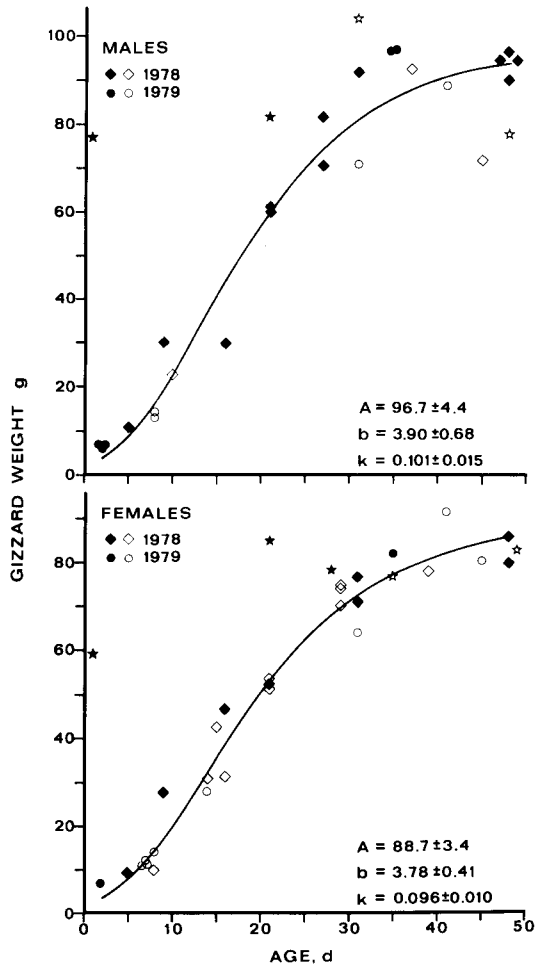
LIPID DYNAMICS

Romanoff (1944) described the decline in visible yolk material after hatching in several species of birds, and Kear (1965) and Marcstrom (1966) documented the dramatic movement of yolk material into the liver of Mallard (*Anas platyrhynchos*) ducklings following hatching. Two- and three-day-old Cackling Goose goslings had very yellow livers containing an average of 0.48 g lipid, which represented 49% of the average liver weight (Fig. 9). Two out of five of these goslings also contained measurable unabsorbed yolk material (0.1 and 0.25 g).

Lipid levels in breast muscles were also highest just after hatching (Fig. 6). Concentrations of lipid in breast muscles declined more slowly than in livers, reaching a stable level of about 10% of breast muscle dry weight at about 30 days of age. Absolute lipid levels in breast muscles did not decline, thus, declining lipid concentrations were due to "dilution" by
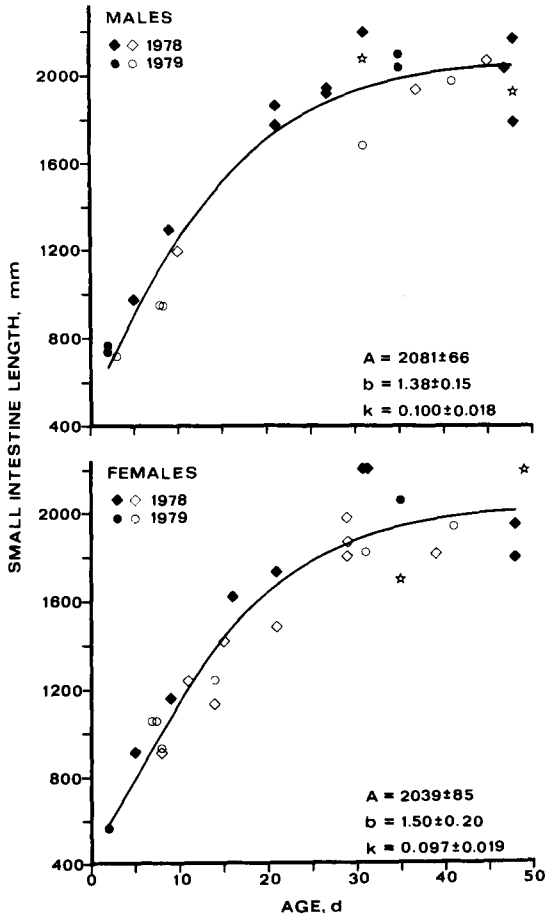
FIGURE 11. Length of small intestines of Cackling Goose goslings. Symbols as in Figure 1.

FIGURE 12. Lengths of ceca of Cackling Goose goslings. Symbols as in Figure 1.

growing muscle tissue. Muscles of adult geese serve as lipid depots (Raveling 1979) and lack of a decline in breast muscle lipid indicates that the muscles of goslings may perform a similar function. As a result of lipid dynamics, total carcass lipid (Marcstrom 1966, Raveling 1979) is probably the best index of the energetic state of goslings during their first week of life.

Two-day-old wild goslings contained an average of 2 g lipid (Fig. 3). Thus, lipid reserves of two-day-old goslings provided 18 kcal of energy (9 kcal/g lipid, Ricklefs 1974). The calculated daily energy requirement for goslings at this age is about 19 kcal/day (calculated from the relationship between BMR and body weight of nonpasserines weighing 61 g [Ricklefs 1974] and multiplying BMR by the extra energy requirement for different activities suggested by King 1974). Therefore, assuming the above estimate of energy requirements was correct, two-day-old goslings could have survived one additional day relying solely on lipid reserves. Daily energy requirement may have been greater than 19 kcal because precocial young have higher metabolic rates than adults of the
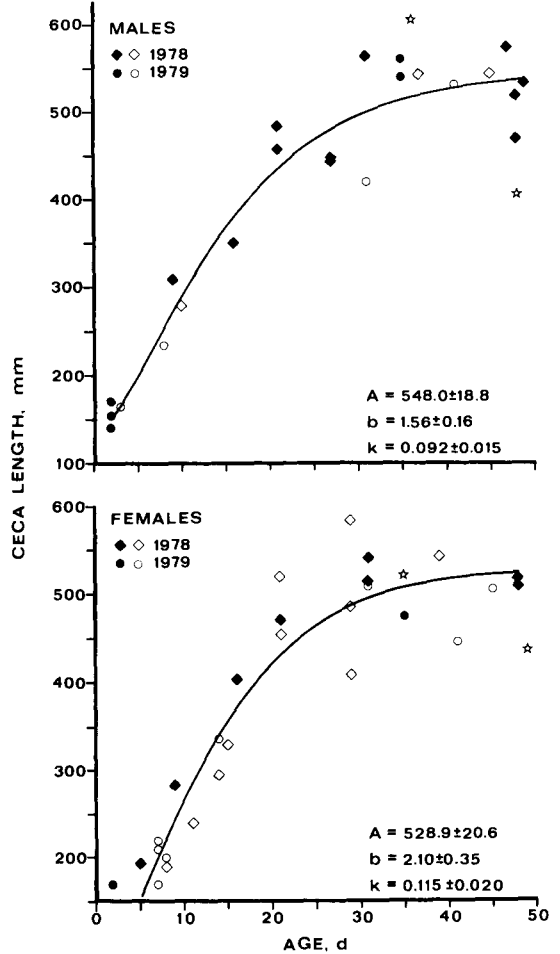
same weight (Ricklefs 1974). Furthermore, some food was eaten during the first two days (pers. observ.), which reduced the need to use lipid reserves to meet energy requirements. Thus, when feeding normally following hatch, Cackling Goose goslings probably had enough lipid reserves to supply their energy requirement for less than three days. This is more than one day less than the survival time of captive Lesser Snow Goose (Chen caerulescens caerulescens) goslings in the absence of food (Ankney 1980), suggesting either that lean tissue may contribute to energy requirements of goslings under extreme conditions or that captive goslings have lower energy requirements than free-ranging goslings. The larger size of Lesser Snow Goose goslings (ca. 85 g at hatch) may have also contributed to their longer survival time by reducing their weight specific energy requirement (Ankney 1980).

PATTERNS OF GROWTH

All elements of the gastrointestinal tract (gizzard, small intestine, ceca) plus livers reached

TABLE 1. Total body weight (g) and relative size (% of total wt.) of organs and muscles in recently hatched, fledged and adult Cackling Geese.

	Recent hatched[a]		Fledged[b]		Adult[c]	
	Male (n = 4)	Female (n = 1)	Male (n = 3)	Female (n = 1)	Male (n = 1)	Female (n = 1)
Total wt. (g)	61.8 ± 1.0[d]	61.4	1,284.3 ± 47.2	1,228.4	1,478.9	1,374.6
Leg muscle	4.2 (2.6 ± 0.2)[e]	4.2 (2.6)	5.7 (71.0 ± 4.1)	6.0 (73.9)	6.8 (101.3)	5.5 (75.4)
Liver	4.5 (2.8 ± 0.3)	4.2 (2.6)	2.7 (33.2 ± 2.5)	2.4 (29.8)	2.0 (29.1)	1.9 (26.4)
Breast muscle	0.5 (0.3 ± 0.1)	0.5 (0.3)	4.9 (61.3 ± 9.5)	6.3 (76.8)	7.6 (112.9)	7.6 (103.9)
Gizzard	10.7 (6.6 ± 0.4)	11.7 (7.2)	7.6 (94.3 ± 1.6)	7.0 (86.5)	5.2 (77.6)	6.1 (83.2)

[a] Recently hatched goslings were 2 (n = 4) or 3 (n = 1) days old.
[b] Fledged goslings were sacrificed 48 or 49 days following the peak of hatch.
[c] Adults were collected coincident with fledging young. Methods were identical to those for goslings.
[d] $\bar{x}$ ± SE.
[e] Values in parentheses are weights (g) of organs or muscles ($\bar{x}$ ± SE).

adult size by about four weeks of age (Figs. 10, 11, 12), which was about three weeks before fledging. This contrasts with patterns in altricial species such as Double-crested Cormorants (Phalacrocorax auritus), where the small intestine and liver reached their asymptotic weights less than one week before total body weight leveled off (Dunn 1975), even though fledging occurred at approximately the same age (6 to 7 weeks; Palmer 1962) as in Cackling Geese (Mickelson 1975). Digestive organs were larger (relative to body weight) at hatching in Cackling Geese than in cormorants. For example, the entire digestive tract of Double-crested Cormorants was approximately 10% or less of total body weight at hatching, whereas the gizzard alone comprised 11% of body weight at hatching in Cackling Geese (Table 1). Chickens also have large gizzards at hatching (12% of body weight; Wilson 1954, 1955). The larger initial relative size of digestive organs in precocial species may explain the slower growth of these organs in precocial as compared to altricial species.

Geese are relatively inefficient at processing their fibrous food (Marriot and Forbes 1970). Hence, they rely on consuming large amounts of food in order to extract sufficient nutrients for growth (Owen 1980). The large initial size and early rapid growth of organs necessary for digesting food and metabolizing nutrients is probably related to the necessity for geese to grow rapidly on a diet that is relatively low in protein content (Owen 1980, Sedinger and Raveling 1984). Plant foods of Cackling Geese contain low levels of sulfur amino acids (Sedinger 1984) and the resulting higher level of protein/amino-acid metabolism required to supply the protein necessary for tissue growth probably accounts for the relatively large livers in goslings (Table 1; Nitsan and Nir 1977). In addition to its digestive function, the gizzard, which is the largest muscle at hatching (Table

1), may be a significant source of heat production, thus assisting thermoregulation.

Leg muscles of Cackling Goose goslings were the same relative size (4.2% of total weight) at hatching as those of Canvasbacks (Aythya valisineria) and Lesser Scaup (Aythya affinis), which were 4.2 to 4.9%, calculated from data in Lightbody and Ankney 1984) but probably relatively smaller than the legs of Japanese Quail (Coturnix coturnix), a smaller, precocial species (16 to 18% of lipid-free weight, Ricklefs 1979). Gosling leg muscles were 6% of body weight at fledging, in contrast to those of ducks, which were only about 1% of body weight at fledging (Lightbody and Ankney 1984). The relatively large leg muscles of geese are indicative of their importance for foraging and predator avoidance in the terrestrial habitats occupied by geese. Leg muscles are considerably smaller (ca. 50 and 60 g in female and male adults, respectively) during the fall and winter when geese are capable of flight (Raveling 1979). The relatively smaller leg muscles of geese (compare Table 1 to Ricklefs 1979) compared to quail may represent a compromise between the requirements for terrestrial locomotion and the necessity to carry the leg muscles on long migratory flights.

Breast muscles developed late and extremely rapidly in Cackling Geese, which was associated with a delay in achievement in mature function as indicated by the water index (Fig. 7). As a result, increased protein in the breast muscles (11 g, Fig. 5) of male goslings accounted for all of the predicted increase in carcass protein (9 g, Fig. 2) from Day 45 to 48. Delayed development of these muscles reduced competition for protein among major protein sinks and allowed maximum early development of the legs and gastrointestinal tract. This may be especially important in geese, because the protein level of the diet consumed by Cackling Geese during much of the growth

period is probably below levels that will sustain maximum growth rates (Sedinger and Raveling, in press). Maximum availability of protein for developing muscle tissue is important because maturation of muscle tissue precludes further proliferation of muscle cells (Holtzer 1970), and nutrient availability during growth can determine the ability of muscle to increase in size in the mature state (Moss et al. 1964, Swatland 1977). Optimization of muscle size is especially important in geese because muscles are principal storage organs for protein reserves used by adults during nest initiation and incubation when little feeding occurs (see Ankney and MacInnes 1978 and Raveling 1979 for a discussion of the role of nutrient reserves in the reproduction of geese). Apparently, the patterns of growth in Cackling Geese represent a compromise between the requirement for mature functioning of particular tissues at particular times and competition for nutrients among the various growing tissues of the young bird (O'Connor 1977).

RATE OF GROWTH

Cackling Goose goslings had growth rates of 0.072 (females) and 0.082 (males) with a combined growth rate for the two sexes of 0.074. These growth rates were higher than those reported for ducks: 0.059 and 0.062 for Canvasbacks and Lesser Scaup, respectively (Lightbody and Ankney 1984); 0.056, Black Ducks, *Anas rubripes* (Reinecke 1979); 0.057, Mallards (reported in Ricklefs 1973), except for one group of Mallards, 0.075 (Sugden et al. 1981). Growth rates of other goose species varied from 0.044 and 0.064 for two groups of Bar-headed Geese (*Anser indicus*), calculated from data in Wurdinger (1975) to 0.078 for Lesser Snow Geese, calculated from data in Ankney (1980). The growth rates of Cackling and Lesser Snow Geese are more than twice those of gallinaceous species of similar size (Ricklefs 1973). Since the leg muscles of waterfowl are relatively smaller than those of gallinaceous birds (see above), these differences in growth rate seem to support Ricklefs' hypothesis that overall growth rate is limited by the proportion of adult weight comprised of tissues that are functionally mature at hatch.

However, comparisons of growth rates within the Anatidae do not support Ricklefs' hypothesis for several reasons. First, leg muscles of Cackling Geese, Lesser Scaup, and Canvasbacks (Lightbody and Ankney 1984, this study) grew at least as fast as the total body. I did not measure water content of the legs of Cackling Geese, and they may not have been fully mature at hatch; but the water indices of the legs of hatching ducklings were at adult levels (Lightbody and Ankney 1984), and this tissue should have been at least as mature in goslings because of the necessity for them to walk within two days of hatching (pers. obs.). Thus, growth rate in these mature tissues did not reduce growth of the carcass as a whole. Second, Cackling Geese grew faster than ducks, despite having legs the same or a larger fraction of total body weight than those of ducks. Finally, comparison of geese that nest at different latitudes suggests that their growth rates may be related to the length of the growing season or daylength during brood rearing. Lesser Snow Geese, which nest between 55 and 72°N, had about the same or a slightly higher growth rate than Cackling Geese, which nest at about 61°N (Mickelson 1975), while Bar-headed Geese, which nest between 34 and 50°N, grew considerably more slowly. Pacific Brant (*Branta bernicla nigricans*) and Barnacle Geese (*Branta leucopsis*) which both nest above 60°N (Owen 1980), fledge at 40 to 50 (Barry 1967, Mickelson 1975) and at 39 days (Owen 1980), respectively, indicating that their rates of growth are similar to those of other arctic nesting geese.

Arctic nesting geese breed in highly seasonal environments, and the most nutritious foods are available for a relatively short time (Sedinger and Raveling, unpubl.). These geese initiate nesting as early as possible, which results in synchronization of gosling growth with the availability of nutritious foods (Raveling 1978b; Sedinger and Raveling, unpubl.). The protein content of the diet begins declining at hatching (Sedinger and Raveling, in press), and protein content of the diet may limit the final size of protein sinks (see above), making it advantageous for goslings to undergo their most rapid growth as early as possible. Because growth early in the postnatal period is a cumulative process, i.e., exponential increase (Laird et al. 1965), the period of most rapid growth occurs about three weeks after hatching in Cackling Geese. However, increasing the rate of growth causes the period of most rapid growth to occur absolutely earlier, hence more synchronously with the availability of nutritious foods. Thus, Ricklefs' hypothesis may explain some of the variability in growth rates among higher phylogenetic groups (i.e., families or orders), but much of the variability in growth rates within these groups may be the result of natural selection attempting to optimize growth patterns within the ecological conditions encountered by individual species as suggested by Lack (1968) and shown by Lightbody and Ankney (1984).

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APPENDIX. Parameter estimates (±SE) resulting from fitting Cackling Goose gosling growth data to the Richards' model.

Gosling component[a]	Parameter estimates			
	A	B	T	M
Total wt, g				
Male	1,234 ± 79	40.5 ± 28.9	41.3 ± 7.1	1.93 ± 0.96
Female	1,177 ± 158	27.5 ± 31.6	52.4 ± 11.4	1.22 ± 0.75
Total protein wt, g				
Male	218.3 ± 19.8	6.15 ± 5.84	41.7 ± 9.7	2.06 ± 1.28
Female	244.3 ± 111.2	5.30 ± 8.02	69.3 ± 41.9	1.14 ± 1.24
Leg muscle wt, g				
Male	71.7 ± 3.9	1.75 ± 2.14	27.2 ± 7.3	2.84 ± 2.20
Female	69.9 ± 6.0	2.25 ± 1.90	39.8 ± 7.6	2.13 ± 1.31
Liver wt, g				
Male	33.6 ± 1.2	2.15 ± 0.93	28.5 ± 5.9	4.08 ± 2.84
Female	34.0 ± 3.9	0.60 ± 1.64	44.6 ± 8.9	0.83 ± 0.78
Gizzard wt, g				
Male	91.6 ± 3.1	6.51 ± 2.40	34.5 ± 5.0	3.00 ± 1.51
Female	86.9 ± 4.3	3.31 ± 2.38	40.8 ± 4.2	1.30 ± 0.56
Small intestine length, mm				
Male	2,015 ± 49	642.5 ± 92.6	47.8 ± 8.2	4.22 ± 3.18
Female	1,962 ± 65	682.5 ± 87.8	55.8 ± 8.5	6.94 ± 6.84
Cecum length, mm				
Male	540.2 ± 22.3	125.6 ± 27.3	46.3 ± 8.5	1.67 ± 1.57

[a] Data from total lipid was not fitted to the Richards' model, and data for breast muscles and female ceca did not converge to a solution.