SEASONAL INFLUENCE ON THE STRATEGIES OF GROWTH AND DEVELOPMENT OF CANVASBACK AND LESSER SCAUP DUCKLINGS

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ABSTRACT.—Eggs of a seasonally early-nesting species of diving duck (Aythyini), the Canvasback (*Aythya valisineria*), and a late-nesting diving species, the Lesser Scaup (*Aythya affinis*), were collected from south-central Manitoba. Ducklings were raised in captivity so that the pattern of growth and development of both species could be examined. Rates of growth of external components were determined in order to test the hypothesis that late-nesting species (scaup) should develop the ability to fly at a younger age and gain weight more slowly than early-hatched species (Canvasback). If Lesser Scaup acquire flight earlier, we predicted that their digestive organs would grow and develop relatively more quickly than those of Canvasbacks, enabling them to process a large amount of food at a younger age. As growth rate is related to adult body size, rates of growth of the smaller Lesser Scaup were scaled to Canvasback size at the asymptote of the juvenile growth curve. Lesser Scaup fledged when they were 6 days younger than Canvasbacks, yet there was no apparent tradeoff in total body growth, as both species fledged at approximately 92% of juvenile asymptotic weight. Flight and leg muscle growth, however, did not differ statistically between species, nor did the change in water content, an indicator of tissue maturity. This is consistent with the idea that tissue maturity, and not the ability to fly, limits growth rate. As we predicted, growth of digestive organs was significantly more rapid in Lesser Scaup than in Canvasbacks. Culmen and tarsus of Lesser Scaup also grew faster than those of Canvasbacks, and we suggest this enables scaup to become efficient foragers more rapidly. The variation in growth rates between species was partially due to the difference in body size. After accounting for this, however, we found that several organs grew faster in Lesser Scaup than in Canvasbacks. Thus, the pattern of development may be influenced by the timing of nesting. *Received 19 November 1982, accepted 1 September 1983.*

PRECOCIAL birds have lower growth rates than altricial birds of similar adult body weight. Lack (1968) proposed that avian growth rates are related to the period of vulnerability of chicks and to food availability and that altricial birds grow quickly in order to get through the stage when they are most vulnerable to predators and adverse weather conditions. Because precocial young are less vulnerable and feed themselves, slow growth rates may reduce their energy requirements to more easily attainable levels. Ricklefs (1968, 1973, 1979a) proposed that growth rate is at a physiological maximum, being limited at the tissue level rather than at the organismal level. He suggested that growth rate is inversely related to precocity of development, or rate of acquisition of mature function of tissues, and that the rate of acquisition of flight may be limiting growth rate. Ricklefs (1979b) also suggested that the length of the postnatal growth period may be related to the amount of growth that the legs have to complete. Species with relatively small legs as adults (e.g. terns) grow faster than those with proportionately large legs (e.g. Japanese Quail, *Coturnix coturnix*, Ricklefs 1979b). This model assumes that tissue is partitioned into mature and embryonic cells and that energy, nutrients, or hormones are not limiting factors.

There has been little research on the patterns of growth in precocial birds, particularly for diving ducks (Tribe Aythyini). There are also few data on the growth of internal organs. Documenting digestive organ development may be important, because processing of food may limit the availability of energy for growth and development (Ricklefs 1973, 1979a). There is great seasonal variation in the time when diving ducks nest, and there may be an evolutionarily important seasonal component in growth rates.

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Within a species, Smart (1965) found that primaries of late-hatched Redheads (*Aythya americana*) emerged a week earlier than those of early-hatched ducklings, and, consequently, the late ducklings fledged at a younger age. Likewise, among species, it may be advantageous for ducklings of late-nesting species to develop faster than those of early-nesting species. Lesser Scaup (*Aythya affinis*) are late nesters, and some ducklings hatch as late as August, which leaves little time to develop the ability to fly before fall migration. On the other hand, Canvasbacks (*Aythya valisineria*) begin nesting in May, and, therefore, selection for early acquisition of flight may not be as strong.

Our objective in this study was to describe the pattern of growth and development in an early- and a late-nesting species of diving duck (Canvasback and Lesser Scaup, respectively) so that we could address the theoretical hypothesis that species of birds that hatch late in the season develop flight early and exhibit a correspondingly slow gain in body weight. We also analyzed data relative to our prediction that if a species developed flight at a younger age, its digestive organs would grow more rapidly than those of a species that develops more slowly.

MATERIALS AND METHODS

Canvasback eggs were collected from nests in the Minnedosa, Manitoba region (50°15′N, 99°50′W) during the first to the third weeks in May 1981. Lesser Scaup eggs were collected from nests in the Interlake district, Manitoba (50°18′N, 97°40′W) during the last week in June and the first week in July 1981; a few Lesser Scaup eggs were collected in the Minnedosa region. Eggs were candled, weighed, and hatched in incubators at the Delta Waterfowl Research Station according to the procedure of Ward and Batt (1973). At hatch, ducklings were sexed and web-tagged for identification.

Ducklings of the same species and of similar age were kept in small groups (<15) in brooder pens and reared according to the procedure of Ward and Batt (1973) until 22 or 23 days of age. Ducklings were then placed in an outdoor pen (9 × 30 m) where they could swim about freely. Because overcrowding may affect growth, the pen was divided into 5 sections (9 × 6 m each) to maintain small (<10) group sizes. A loafing bar was provided in each section, and a large food dish was placed on it.

A commercial duck food (Feed Rite custom mix) was fed *ad libitum* throughout the experiment. Upon transfer to the outdoor pen, ducklings were fed a 50:50 mixture of commercial food and wheat. We assumed that Canvasback and Lesser Scaup utilized this food equally efficiently, because wild ducklings of both species have similar food requirements, chiefly invertebrates (Collias and Collias 1963, Bartonek and Hickey 1969, Sugden 1973). Continuous cycling of slightly chlorinated water in the pens kept invertebrates to a minimum; thus, we feel certain that the ducklings were not ingesting enough invertebrates to affect their growth.

Measurements of the ducklings were first taken at day 0 (hatch). Ducklings were then measured every other day until day 14, or they were measured at hatch and on day 1 and then on alternate days until day 13 if they hatched on days between "routine" measuring days. After day 14 (or 13), measurements were taken every 4 days. Weight was measured to the nearest 0.1 g with a Mettler digital pan balance until day 22 or 23 (day of transfer to the outdoor pen) and to the nearest 10 g with a Pesola spring scale thereafter. Ducklings were weighed at the same time each day to avoid a bias caused by diurnal changes in weight (Blake 1956) and were placed in a nylon stocking to restrict their movement while being weighed. Linear measurements of the tarsus (tarsometatarsus including head of the tibiotarsus), culmen (from most distal feather of forehead to bill tip), and bill width (widest point distal to nares) were taken to the nearest 0.05 mm with calipers. Wing (proximal end of the metacarpal to distal tip of phalanges) and ninth primary (excluding shaft) were measured to the nearest 1.0 mm with a ruler. The wing was measured by holding it flat and straight against the ruler. All measurements were taken until the shafts of all primaries were firm and clear (fledging), as described by Weller (1957).

Eight birds of each species were killed and frozen on each of days 0, 7, 14, 21, 31, 41, 51, and 71 for carcass analysis. At hatch, ducklings were assigned to be killed at a particular age in a stratified random manner by assigning each duckling a number (0 to 8) from a random numbers table to represent the date of sampling. Four ducklings of each sex were assigned to a period before it was considered full. If a duckling from one clutch was assigned to a particular sample period and then one of its siblings drew the same number or if the sample period was full, another random number was chosen. This stratified sampling ensured that ducklings in each sample were all from different clutches, had a 50:50 sex ratio, and were of equal number. Some samples contained fewer than 8 birds, because some ducklings died at hatch or shortly thereafter.

Flight muscles (pectoralis, coracobrachialis, supracoracoideus, biceps, triceps, and other small muscles), leg muscles (gastrocnemius, tibialis, peroneus longus, biceps, semimembranosus, and other small muscles), and internal organs (proventriculus, gizzard, intestine, caeca, liver, heart) were oven dried

TABLE 1. Growth rates (K) and time (days) to grow from 10 to 90% of adult size (in parentheses) of external components of Lesser Scaup and Canvasbacks. Significance values are from *F*-tests for equality of slopes of the transformed growth curves, a comparison of growth rates.

Measurement	Growth rate (K)			*P*
	Lesser Scaup		Canvasback	
	US[a]	S[b]		
Weight	0.0622 (50)	0.0535 (58)	0.0592 (52)	NS
Wing length	0.0988 (44)	0.0952 (46)	0.0896 (49)	<0.001
Primary 9	0.196 (22)	0.186 (24)	0.181 (24)	<0.001
Tarsus	0.0873 (35)	0.0818 (38)	0.0761 (41)	<0.001
Culmen length	0.0718 (38)	0.0643 (43)	0.0549 (50)	<0.001
Bill width	0.0661 (41)	0.0677 (40)	0.0578 (47)	<0.001

[a] US = unscaled.
[b] S = scaled to Canvasback size.

at 100°C for 24 h. Drying at this temperature has been shown not to change the lipid content of the tissues (Kerr et al. 1982). Intermuscular fat was removed from all tissues before drying. Caecae were not measured at hatch, because they were too small to dissect accurately or precisely; they are included in the intestine weight. All organs were weighed to the nearest 0.01 g on a Sartorius pan balance before and after drying. Mean values of water content of flight and leg muscle were generated, and a "water ratio" was calculated as water content/dry weight for each sample. This underestimates water ratio, because the dry weight includes lipid weight, and changes in lipid content with growth may bias interpretations of this index.

Males and females were pooled for all analyses, as differences in all measurements were found to be minimal until about day 71 (Lightbody 1982). Sample means for each component of both species were graphed, and curves were drawn through the points by eye. To determine whether a curve was best described by the Logistic, Gompertz, or von Bertalanffy equation, each growth curve (means for every measurement day) was transformed to a straight line following the procedure of Ricklefs (1967). This method of fitting curves is not as accurate as a least squares nonlinear method, but it is adequate for tests between species where the difference in slopes is large relative to error. Degrees of freedom differ among curves, because only the portion of the growth curve up until maximum size was used in the transformation and subsequent tests for equality of slopes. The slope of the transformed curve is proportional to the overall growth rate, and slopes were compared statistically using a standard formula in Sokal and Rohlf (1969: 450). "Adult" size of all components was considered to be the asymptote of the juvenile growth curves. Juvenile asymptote has been shown to correspond very well with true adult size (the same birds, 1 yr old) in Redheads, and our asymptotic values correspond closely with values obtained from captive (wild eggs or first generation captive) adult Canvasbacks and Lesser Scaup (Lightbody unpubl. data). The asymptotic body weight is probably an underestimate of true adult weight, which includes more fat.

A growth rate constant (K), which takes into account the form of the curve, was calculated from the growth equation, and the time to grow from 10% to 90% ($t_{10\text{-}90}$) of asymptotic size was determined for each measurement (after Ricklefs 1967). Because adult body weight (W) (taken as asymptotic in this study) and growth rate (K) are related by the equation $K = aW^b$, where a and b are constants [Ricklefs (1973), we estimated from Ricklefs (1973) that, in waterfowl, b is approximately −0.28], growth rates of Lesser Scaup were scaled to Canvasback asymptotic size. A 10% error in the estimation of b would result in a 1% error in the scaled growth rates. The equation used to scale was $K_2 = K_1 (X/X')^{-0.28}$, where K_1 and K_2 are the old and the new rates, respectively, X = adult (asymptotic) size of the component of the larger species (Canvasback), and X' = asymptotic size of the component of the smaller species (Lesser Scaup). A growth index was calculated for each species based on the time to grow from 10 to 50% of asymptotic body weight (Ricklefs 1967). Each growth curve was plot-

TABLE 2. Age when shafts of the primaries started to clear and were all clear (fledging) and percentage of juvenile asymptotic weight at fledging for Lesser Scaup and Canvasback ducklings. Standard errors in parentheses.

	Age (days) when shafts		Percentage asymptotic weight at fledging
	Started to clear	All clear	
Lesser Scaup ($n = 7$)	49 (0.96) $F = 15.45$, $P < 0.005$	65 (0.91) $F = 33.53$, $P < 0.005$	92.9 (2.62) $F = 0.005$, $P > 0.05$
Canvasback ($n = 6$)	57 (1.07)	71 (0.61)	92.5 (2.0)

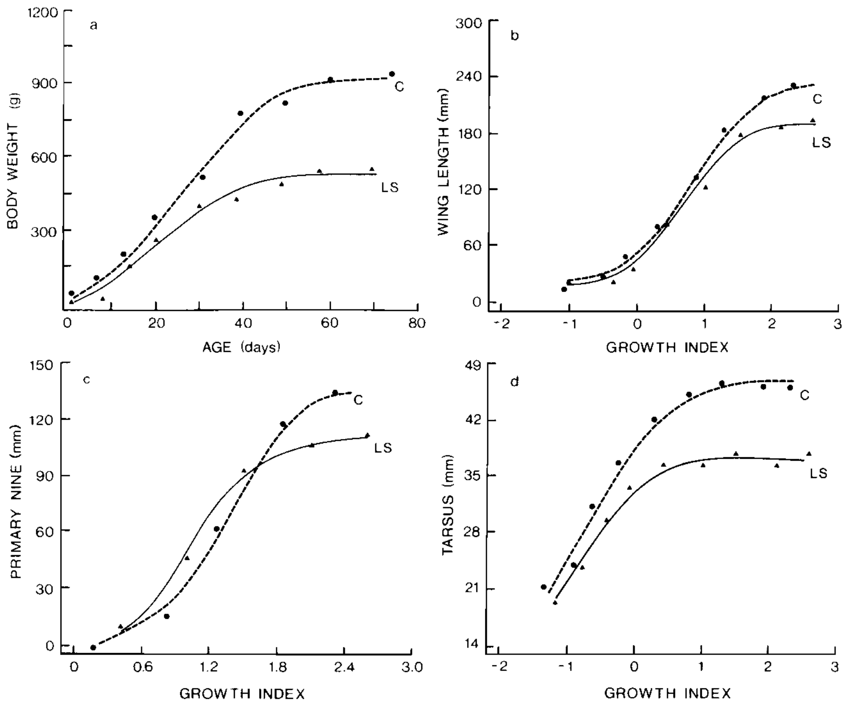

Fig. 1. Growth curves for Lesser Scaup (LS) and Canvasback (C) ducklings: (a) body weight, curves were best fit by the Gompertz equation; (b) wing and (c) ninth primary, curves were best fit by the Logistic equation; (d) tarsus, curves were described by the von Bertalanffy equation. See text for an explanation of growth index. For clarity of presentation, only weekly mean values are plotted. Standard errors of the means are presented in the Appendix.

ted as a function of the species' corresponding growth indices, which adjusts the time scale (age) by body growth to make the curves coincide along the abscissa. The growth index "0" represents the point at which 50% of asymptotic weight is reached. Only weekly mean values for each component were plotted; means and standard errors for all components are presented in the appendix.

One-tailed analyses of variance were done to test the null hypotheses that (1) ages at fledging did not differ between species and (2) percentages of adult (asymptotic) weight at fledging did not differ between species.

RESULTS

External measurements and mature function.— Body-weight growth rate up to the juvenile asymptote did not differ between species (Table 1, Fig. 1a). Lesser Scaup had higher growth rates (Table 1) of wing length, primary 9 (Fig. 1b, c), and tarsus (Fig. 1d) than did Canvasbacks. The time for these components to grow from 10 to 90% of asymptotic size was shorter for Lesser Scaup (Table 1). All three components attained asymptotic size before time of fledging. The difference in size of the two species accounted for some of the variation in growth rates, but Lesser Scaup still had the highest values (Table 1).

Lesser Scaup were at a younger age than Canvasbacks when shafts of the primaries started to clear (Table 2). The percentage of asymptotic weight attained at fledging did not differ between species (Table 2); growth indices at fledging were 2.23 for Lesser Scaup and 2.26 for Canvasbacks.

Growth of flight muscles did not differ between species (Table 3, Fig. 2a). Asymptotic size had not been approached by the final sample day, but, because body weight had approached its asymptote, we assumed the flight muscle had very nearly reached its final size by day 71. There was no difference between species in rate of growth of leg muscles (Table 3, Fig. 2b). However, $t_{10\text{-}90}$ was slightly less for Lesser Scaup

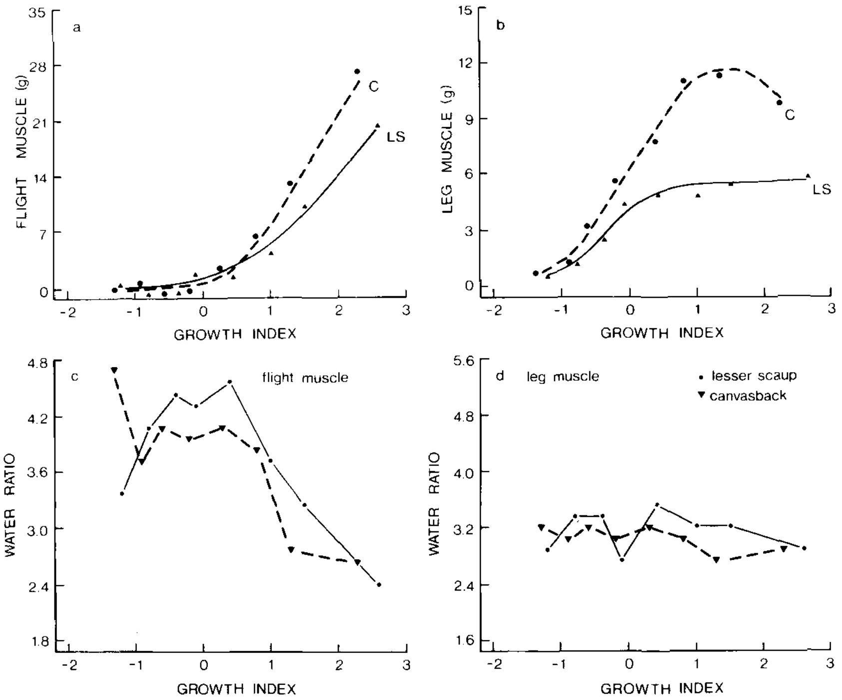

Fig. 2. Growth of Lesser Scaup (LS) and Canvasback (C) ducklings: (a) flight muscles, curves were described by the Logistic equation, with the assumption that size at day 71 was close to the asymptote; (b) leg muscles, curves were described by the Gompertz equation. Change in water ratios (water content/dry weight) of (c) flight and (d) leg muscles. See text for an explanation of growth index. Standard errors of the means are presented in the Appendix.

(Table 3). There was a slight drop in leg muscle dry weight for Canvasbacks on day 71. Change in water ratio of flight and leg muscles with age was similar for both species (Fig. 2c, d; ranges overlap considerably but are not plotted), but curves differed between flight and leg muscles. At hatch, water content of leg muscles was proportionately the same as at asymptotic size, indicating that leg muscles were functionally well developed at hatch. That was not true of flight muscles, as the ratio declined during growth. Owing to the small size of flight muscles at hatch, variation in water ratio was high for this sample (range of 3.0–7.0 for Canvasback and 2.6–4.4 for Lesser Scaup). Thus, the difference between species at hatch is probably not real.

The culmen (length and width) of Lesser Scaup grew faster than that of Canvasbacks (Table 1, Fig. 3). This pattern was similar even after accounting for the difference in adult size of the birds. Culmen length and width attained asymptotic size before Lesser Scaup ducklings fledged; culmen width reached asymptotic size before Canvasback ducklings fledged, but culmen length did not.

Digestive organs.—The growth rate of the proventriculus did not differ between species (Table 3, Fig. 4a). Growth rates of the gizzard, caeca, and intestine (weight and length) were significantly greater for Lesser Scaup than for Canvasbacks (Table 3, Fig. 4b–e). This pattern was still evident after scaling for adult size. The $t_{10\text{-}90}$ values also remained lower for Lesser Scaup after scaling (Table 3). Growth rates of the heart and liver did not differ between species (Table 3, Fig. 5). Proportionate size of organs was higher at hatch than at fledging, except for the gizzard (Table 4). At hatch, the organs of Lesser Scaup were proportionately larger than, or at least equal to, those of Canvasbacks. For both species there were decreases in size of internal organs from day 51 to day 71 (Table 5). Fewer of these decreases were sta-

TABLE 3. Growth rates (K) and time to grow from 10 to 90% of adult size (in parentheses) of internal components of Lesser Scaup and Canvasback ducklings. Significance values are from *F*-tests for equality of slopes of the transformed growth curves, a comparison of growth rates.

	Growth rate (K)			
	Lesser Scaup			
Measurement	US[a]	S[b]	Canvasback	*P*
Flight muscle dry weight	0.127 (35)	0.118 (37)	0.128 (34)	NS
Leg muscle dry weight	0.0962 (32)	0.0805 (38)	0.0777 (40)	NS
Proventriculus dry weight	0.0920 (30)	0.0859 (32)	0.0916 (30)	NS
Gizzard dry weight	0.0781 (35)	0.0763 (36)	0.0553 (50)	<0.05
Caeca dry weight	0.122 (22)	0.104 (26)	0.0814 (34)	<0.01
Intestine dry weight	0.104 (26)	0.0929 (30)	0.0776 (35)	<0.05
Intestine length	0.0952 (29)	0.0931 (29)	0.0601 (46)	<0.05
Liver dry weight	0.0659 (42)	0.0542 (51)	0.0531 (52)	NS
Heart dry weight	0.0430 (64)	0.0362 (76)	0.0373 (73)	NS

[a] US = unscaled.
[b] S = scaled to Canvasback size.

tistically significant for Lesser Scaup. There was no decrease in heart weights, which had not attained asymptotic size by day 71 (Fig. 5a).

DISCUSSION

This study supported the prediction that a late-nesting species should exhibit a more precocial type growth pattern and develop flight earlier than an early-nesting species. The wing and primaries of Lesser Scaup grew faster and scaup fledged when they were 6 days younger than Canvasbacks, yet both species fledged at the same percentage (92%) of juvenile asymptotic weight. This suggests that the acquisition of flight is not limiting growth rate. The asymptotic weights we found are lower than adult weights recorded elsewhere (Johnsgard 1975, Bellrose 1980). Using these weights, we found that Lesser Scaup fledged at 530/800 g = 66% adult weight, and Canvasbacks at 912/1,200 g = 76% adult weight. Therefore, there may be some cost associated with attaining flight earlier in Lesser Scaup. We feel, however, that the autumn juvenile weight is a more useful value for comparisons, as this is the weight at which the birds must migrate.

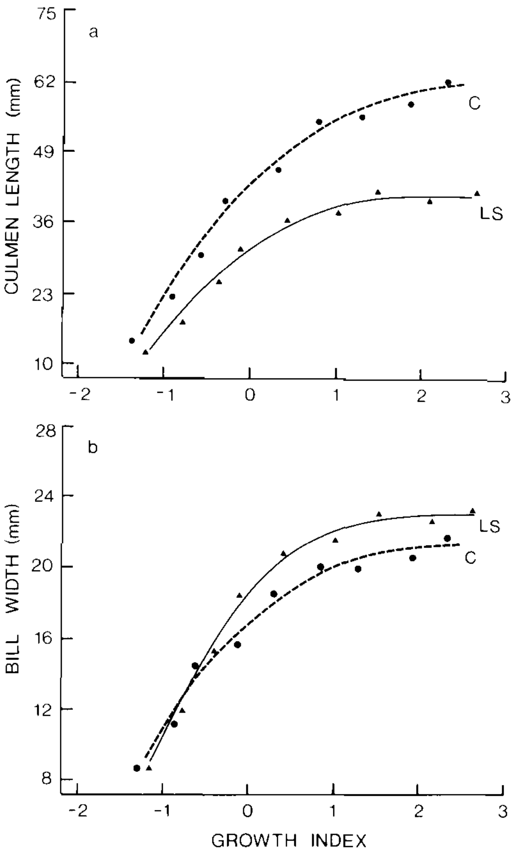

Fig. 3. Growth of (a) culmen length and (b) bill width of Lesser Scaup (LS) and Canvasback (C) ducklings. Growth of both components was described by the von Bertalanffy equation. See text for an explanation of growth index. For clarity of presentation, only weekly mean values are plotted. Standard errors of the means are presented in the Appendix.

Change in water content and growth of flight muscles did not differ between species, indicating that these muscles matured at the same rate for both species and that scaup can fly with less developed muscles than can Canvasbacks. As Canvasbacks have higher wing loading than Lesser Scaup, age at fledging may be greater, because flight muscles have to grow for a longer time to become proportionately larger than those of Lesser Scaup. Differences in the change in fat content between flight and leg muscles could produce the "water ratio" curves we cal-

TABLE 4. Proportionate size (mean and standard deviation) of digestive organs of Lesser Scaup and Canvasback ducklings at hatch and at fledging.

	Percent of total body weight					
	Lesser Scaup		Canvasback			
Organ	Hatch	Fledging	Hatch	Fledging	*t*	
n	8	6	7	7		
Proventriculus	0.6 (0.2)	0.34 (0.03)	0.42 (0.05)	0.23 (0.03)	2.31 $P < 0.05$	6.47 $P < 0.001$
Gizzard	2.9 (0.5)	3.9 (0.4)	2.1 (0.2)	1.9 (0.3)	4.0 $P < 0.01$	12.5 $P < 0.001$
Intestine	2.1 (0.5)	1.4 (0.2)	1.5 (0.3)	1.0 (0.2)	2.73 $P < 0.05$	3.33 $P < 0.01$
Caeca	0.18 (0.04)[a]	0.08 (0.02)	0.19 (0.06)[a]	0.06 (0.02)	0.38 $P > 0.05$	1.67 $P > 0.05$

[a] Values taken at 7 days old.

culated without a change in actual water content. The decline in water ratio of the developing muscle is consistent with other studies, however, which used lean dry weight as the denominator (Ricklefs 1975, 1979b). This supports our interpretation that the curve is mainly a result of decreasing water content. Our results are consistent with Ricklefs' (1973, 1979a) proposal that the rate of muscle maturity (as indicated by muscle growth and water content) limits growth rate, as the two species did not differ in either regard. We suggest that the ability to fly is not a good indicator of muscle maturity, only of the muscle size required for a particular wing load.

The values for body growth rate in this study are slightly higher than the values for another diving duck (the Redhead: Weller 1957, recalculated by Ricklefs 1973), but do not differ from the value one of us found (Lightbody unpubl. data), and for a dabbling duck [Tribe Anatini, the Mallard (*Anas platyrhynchos*): Dement'ev and Gladkov 1952 in Ricklefs 1979]. Yet, they are lower than values calculated for two other dabbling ducks [Gadwall (*Anas strepera*): Oring 1968, recalculated by Ricklefs 1973; and Black Duck (*Anas rubripes*): Reineke 1979], and another nondiving species [Tribe Cairinini, the Wood Duck (*Aix sponsa*): Fendley and Brisbin 1977]. Diving ducks may have a higher energetic cost for thermoregulation and development of insulative feathers than do dabbling ducks, which would reduce the amount of energy available for growth (Ricklefs 1973).

TABLE 5. Between-day comparisons of mean sizes of digestive organs at ages 51 and 71 days for Lesser Scaup and Canvasbacks.

		Lesser Scaup			Canvasback		
Measurement[a]	Day	*n*	Mean	*P*	*n*	Mean	*P*
Proventriculus dry weight	51	7	0.450	NS	8	0.617	<0.05
	71	6	0.407		7	0.499	
Gizzard dry weight	51	7	6.711	NS	8	6.771	<0.01
	71	6	5.598		7	4.643	
Caeca dry weight	51	7	0.110	<0.05	8	0.208	<0.01
	71	6	0.085		7	0.134	
Intestine dry weight	51	7	1.884	NS	8	2.841	<0.05
	71	6	1.747		7	2.114	
Intestine length	51	7	143.3	<0.05	8	146.5	<0.05
	71	6	133.2		7	131.6	
Liver dry weight	51	7	6.379	NS	8	11.72	NS
	71	6	5.945		7	10.00	

[a] Values are in cm for intestine length and in g for all others.

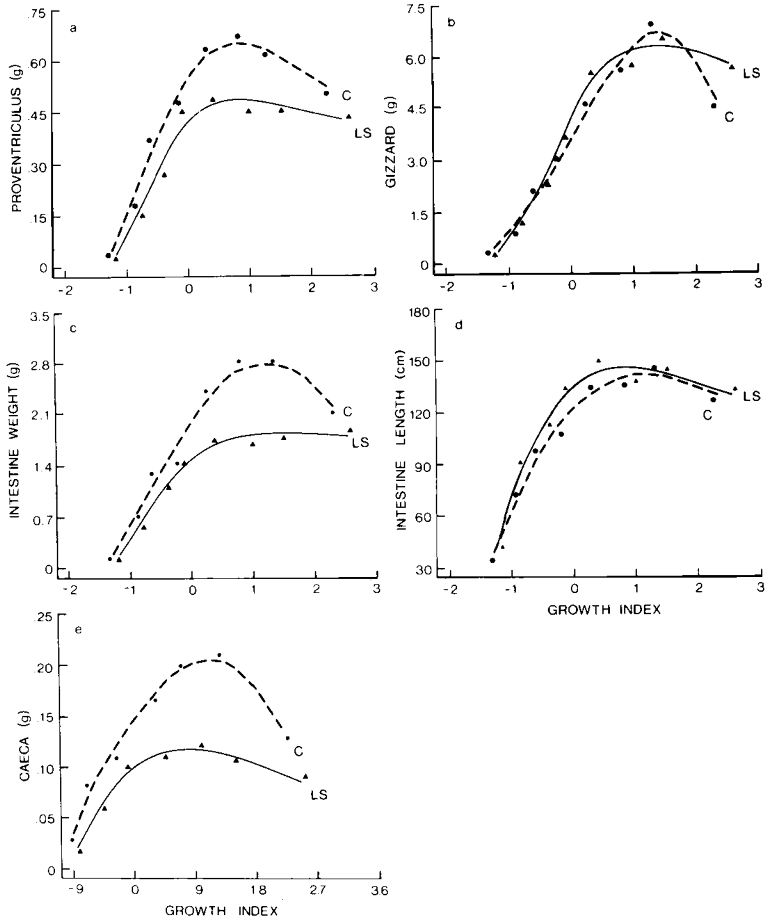

Fig. 4. Growth of the digestive organs of Lesser Scaup (LS) and Canvasback (C) ducklings: (a) proventriculus, (b) gizzard, (c) intestine weight, (d) intestine length, (e) caeca. All curves, using only the portion up to the point of maximum size, were described by the von Bertalanffy equation. See text for an explanation of growth index. Standard errors of the means are presented in the Appendix.

Ricklefs (1979b) and Ricklefs et al. (1980) suggested that total body growth rate is related to the amount of growth in leg muscles between size at hatching and adult size. Diving ducks have proportionately larger legs than do dabbling ducks, which would also contribute to the difference in growth rates between the two tribes. We expected that growth and development of the leg muscles would be similar for Canvasbacks and Lesser Scaup, because the leg muscles of both species are proportionately similar in size at hatch and as adults. Neither the growth nor change in water ratio of leg muscles differed between species, which is also consistent with Ricklefs' (1973, 1979a) idea that maturity limits growth rate. The leg muscle water ratio did not change throughout growth, supporting our idea that these muscles were functionally well developed at hatch. We found that the tarsi of Lesser Scaup grew more rapidly than those of Canvasbacks, however. We suggest that this enables scaup to become efficient foragers at a younger age than Canvasbacks.

In previous studies, culmen growth was similar in Canvasbacks (Dzubin 1959) and Redheads (Weller 1957). We found that the culmen of Lesser Scaup grew more rapidly than that of Canvasbacks. Ducks' bills are highly specialized for aquatic feeding, so scaups' bills may

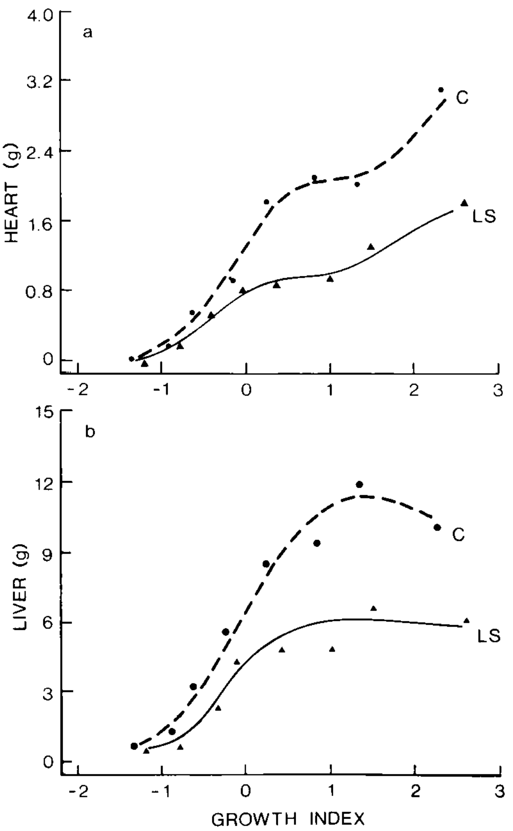

Fig. 5. Growth of (a) the heart and (b) the liver of Lesser Scaup (LS) and Canvasback (C) ducklings. All curves, using only the portion up to the second point of inflection, were described by the Gompertz equation. See text for an explanation of growth index. Standard errors of the means are presented in the Appendix.

grow rapidly to maximize their foraging efficiency. In species that are parentally fed, bill growth is slow, and it is often well below adult size at fledging (Kahl 1962, Dunn 1975, Kushlan 1977, Caccamise 1980).

The rate of development and assimilation efficiency of digestive organs can potentially limit the rate at which energy is made available to cells. Altricial species have disproportionately large digestive organs, which grow rapidly, and Dunn (1975) suggested that this enables them to process a lot of food relative to body size. O'Connor (1977) also found that the greatest increase in digestive organ size corresponded to the period of most rapid overall growth in passerines. Digestive organs of Lesser Scaup grew faster and were proportionately larger throughout growth than those of Canvasbacks. Intestine and caeca were the most rapidly growing organs of both species, which indicated a high demand for food processing. There is evidence that the intestine is longest when a bird is feeding heavily (Fell 1969, Moss 1972, Ankney 1977). There was no difference between species in growth of the proventriculus, but its growth was similar to or higher than that of other organs. The liver growth rate did not differ between species, but the liver grew more slowly than other organs, which may indicate that it was relatively well developed at hatch and had little growth left to complete. Lean tissue growth rate may have been higher though, as the livers of young goslings (McLandress pers. comm.) and Tufted Ducks (*Aythya fuligula*, Kear 1970) contain a lot of lipid.

All digestive organs, except the liver, exhibited a decrease in size between the last two sample days (day 51 and 71). Organ size decreased less over this period in Lesser Scaup than in Canvasbacks, because their organs had already begun to decrease by day 51. Possibly, this decrease was due to a shift in protein allocation to leg and flight muscles. The heart appeared to be reaching an asymptotic weight just before ducklings fledged, but, after they fledged, its growth rate increased. There was no difference between species in heart growth rate, perhaps because there were similar demands on the heart related to overall activity, not just to digestion. The heart grew slowly, which suggests that it is functionally well developed at hatch.

There may be competition for energy between growth (embryonic tissue) and function (mature tissue) of the various components. Ricklefs' (1973, 1979a) model assumes that cells are metabolizing energy and nutrients as fast as possible and that this limits growth rate. Although our results of leg and flight muscle maturity are consistent with this model, we feel that there is a limit on the total amount of energy available to partition among components; otherwise, all components of Canvasbacks should grow as fast as those of scaup.

A higher overall growth rate, and faster growth of specific components, could be achieved if a species could consume more, or assimilate more efficiently. Several factors have been shown to effect such changes. Genes that cause more efficient assimilation of food and influence feeding rates influence growth rates in swine, rats, and cattle (Dickerson 1954). Injection of growth hormone or thyroxine can increase feeding rate and growth efficiency in vertebrates (Premachandra et al. 1959, Licht and Hoyer 1968, Brown et al. 1974, Bentley 1976). Proximate conditions may affect the level of growth hormone secreted. Premachandra et al. (1959) and Stahl et al. (1961) found that warm temperature decreased thyroxine secretion rate in chickens. We suggest that daylength could influence hormone secretion as well. In the wild, Lesser Scaup grow under longer daylengths and generally lower temperatures than Canvasbacks, because they tend to nest farther north. Therefore, Lesser Scaup may grow even faster under natural conditions.

The general pattern of growth rates over all precocial and altricial species of birds supports Ricklefs' idea that cells are partitioned between growth and mature function, and growth is limited by tissue constraints. The numerous exceptions to the model support Lack's idea that there are some environmental limitations that can act ultimately or proximately to produce an optimum, not necessarily a maximum, growth rate. Selection can also act on a species' pattern of development such that the most important components develop the earliest (O'Connor 1977), possibly at the expense of overall growth rate. Some of the variation between species' growth rates of various body components in this study was accounted for by the difference in adult size of the birds. Lesser Scaup are able to nest as late as they do partially because they are small and can grow, develop, and fledge quickly. There does appear to be an environmental influence related to the timing of nesting that "fine tunes" the general precocial pattern of development such that several components of Lesser Scaup grow relatively faster than those of Canvasbacks. This "fine tuning" may be a result of higher energy intake, a more efficient digestive system, more efficient use of energy by the tissues, or of an increase in secretion of growth hormone, but the mechanism remains to be determined. Further work is necessary to determine whether or not other species support our prediction and whether or not mid-season hatched young exhibit an intermediate growth pattern.

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APPENDIX. Means and standard errors of external and internal components of Lesser Scaup and Canvasback ducklings.

Measurement	Species[a]	Age (days)								
		0	7	14	21	31	41	51	62	71
External										
Culmen length	LS	13.3	19.0	25.2	31.2	35.0	37.4	41.1	40.5	41.1
(SE)[b]		(0.07)	(0.21)	(0.23)	(0.47)	(0.33)	(1.19)	(0.35)	(0.36)	(0.57)
	C	16.2	22.9	32.1	38.3	46.9	53.7	57.1	60.0	60.7
(SE)		(0.19)	(0.24)	(0.49)	(0.60)	(0.33)	(0.99)	(0.54)	(0.67)	(0.71)
Bill width	LS	9.2	12.2	15.4	18.3	20.5	21.6	23.2	22.9	23.5
(SE)		(0.04)	(0.13)	(0.12)	(0.25)	(0.21)	(0.43)	(0.31)	(0.18)	(0.23)
	C	8.6	11.1	14.1	16.0	18.3	19.8	20.3	21.0	21.3
(SE)		(0.04)	(0.09)	(0.12)	(0.17)	(0.09)	(0.21)	(0.10)	(0.18)	(0.19)
Weight	LS	31.9	74.0	159.6	286.7	376.2	430.0	523.7	528.0	543.3
(SE)		(0.42)	(2.18)	(3.67)	(12.6)	(14.7)	(51.2)	(29.0)	(0.86)	(7.15)
	C	41.4	88.3	214.3	364.0	549.8	775.0	888.0	908.7	912.0
(SE)		(0.52)	(2.26)	(5.98)	(13.9)	(12.1)	(13.0)	(26.5)	(21.2)	(2.85)
Wing length	LS	17.1	18.2	23.4	39.4	88.8	122.2	178.7	192.8	196.8
(SE)		(0.07)	(0.12)	(0.32)	(1.73)	(4.22)	(1.67)	(2.53)	(2.27)	(2.26)
	C	17.2	18.1	22.2	30.7	71.0	133.3	178.1	215.4	226.8
(SE)		(0.11)	(0.13)	(0.28)	(1.29)	(2.60)	(4.71)	(3.57)	(3.60)	(2.85)
Ninth primary	LS					8.9	46.2	92.1	110.6	112.5
(SE)						(1.41)	(7.64)	(3.23)	(0.24)	(1.33)
	C					1.0	17.3	58.4	116.0	129.2
(SE)						(1.00)	(2.50)	(3.56)	(5.04)	(2.60)
Tarsus	LS	19.2	23.1	28.8	33.5	35.7	36.1	37.5	36.8	37.1
(SE)		(0.09)	(0.23)	(0.25)	(0.48)	(0.37)	(0.45)	(0.51)	(0.60)	(0.62)
	C	21.0	23.9	30.8	36.9	42.6	44.5	45.8	46.0	46.0
(SE)		(0.15)	(0.21)	(0.27)	(0.49)	(0.21)	(0.61)	(0.28)	(0.47)	(0.43)
Internal										
Flight muscle	LS	0.05	0.10	0.22	0.70	1.25	3.65	10.03		19.80
(SE)		(0.00)	(0.01)	(0.02)	(0.05)	(0.19)	(1.00)	(1.00)		(1.08)
	C	0.03	0.10	0.21	0.53	1.90	5.08	13.00		26.44
(SE)		(0.00)	(0.01)	(0.02)	(0.02)	(0.14)	(0.21)	(1.42)		(0.74)
Leg muscle	LS	0.40	1.00	2.32	5.28	4.75	5.06	5.67		5.76
(SE)		(0.02)	(0.08)	(0.19)	(0.57)	(0.21)	(0.71)	(0.38)		(0.17)
	C	0.42	1.08	2.88	5.19	7.87	10.52	11.14		9.86
(SE)		(0.02)	(0.13)	(0.16)	(0.10)	(0.38)	(0.21)	(0.71)		(0.28)

APPENDIX. Continued.

Measurement	Species[a]	Age (days)								
		0	7	14	21	31	41	51	62	71
Intestine weight	LS	0.13	0.59	1.07	1.45	1.74	1.73	1.88		1.75
(SE)		(0.00)	(0.04)	(0.06)	(0.11)	(0.16)	(0.09)	(0.08)		(0.11)
	C	0.13	0.65	1.22	1.41	2.40	2.82	2.84		2.11
(SE)		(0.01)	(0.11)	(0.07)	(0.06)	(0.17)	(0.21)	(0.26)		(0.16)
Intestine length	LS	42.6	92.4	112.4	129.7	147.3	139.7	143.3		133.2
(SE)		(3.4)	(3.2)	(2.2)	(2.9)	(4.9)	(2.2)	(2.8)		(3.4)
	C	33.7	70.7	97.3	109.9	130.2	139.5	146.5		131.6
(SE)		(0.9)	(2.5)	(2.2)	(1.9)	(2.8)	(2.5)	(4.0)		(4.1)
Proventriculus	LS	0.04	0.16	0.28	0.44	0.49	0.46	0.45		0.41
(SE)		(0.00)	(0.01)	(0.02)	(0.02)	(0.05)	(0.01)	(0.03)		(0.01)
	C	0.03	0.18	0.35	0.47	0.62	0.66	0.62		0.50
(SE)		(0.00)	(0.02)	(0.02)	(0.01)	(0.02)	(0.04)	(0.02)		(0.02)
Gizzard	LS	0.17	1.15	2.45	3.45	5.38	5.65	6.71		5.60
(SE)		(0.01)	(0.06)	(0.21)	(0.28)	(0.58)	(0.32)	(0.91)		(0.25)
	C	0.19	0.95	2.01	2.94	4.36	5.57	6.77		4.63
(SE)		(0.01)	(0.10)	(0.10)	(0.15)	(0.16)	(0.45)	(0.49)		(0.34)
Caeca	LS		0.02	0.06	0.10	0.11	0.12	0.11		0.08
(SE)			(0.00)	(0.00)	(0.01)	(0.02)	(0.01)	(0.01)		(0.01)
	C		0.03	0.08	0.11	0.17	0.20	0.21		0.13
(SE)			(0.00)	(0.01)	(0.00)	(0.01)	(0.01)	(0.01)		(0.02)
Liver	LS	0.35	0.89	2.16	4.04	4.65	4.55	6.38		5.94
(SE)		(0.02)	(0.07)	(0.18)	(0.44)	(0.38)	(0.46)	(0.47)		(0.44)
	C	0.37	1.17	3.20	5.43	8.65	9.90	11.72		10.00
(SE)		(0.04)	(0.15)	(0.17)	(0.37)	(0.58)	(0.68)	(0.58)		(0.58)
Heart	LS	0.07	0.18	0.45	0.63	0.76	0.91	1.24		1.71
(SE)		(0.01)	(0.01)	(0.07)	(0.03)	(0.06)	(0.11)	(0.05)		(0.12)
	C	0.06	0.20	0.51	1.03	1.77	2.03	2.10		3.05
(SE)		(0.00)	(0.02)	(0.04)	(0.07)	(0.08)	(0.11)	(0.08)		(0.25)

[a] LS = Lesser Scaup; C = Canvasback.
[b] SE = standard error.