GROWTH, BODY COMPONENTS AND ENERGY CONTENT OF NESTLING DOUBLE-CRESTED CORMORANTS

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Most growth studies are confined to measurement of weight gain and external measurements, but the growth process involves a great many internal changes as well. As precocial chicks are much more mature at hatching than altricial young, it is not surprising that their internal and external development differs (Ricklefs 1973, 1974). But growth processes also vary among species of the same developmental mode, and detailed studies should be of value in analyzing differences in ecological adaptation (Dunn 1973, 1975b).

This paper presents the results of a detailed study on growth of nestling Double-crested Cormorants, *Phalacrocorax auritus*. (Unless otherwise noted, all references here to cormorants mean this species.) Measurements were taken of overall weight gain, several external linear dimensions, growth of internal organs, changes in fat and water content, and caloric density. Although primarily a descriptive paper, comparisons are drawn to data for other species and basic differences between precocial and altricial development are noted. The cormorant is the largest altricial species studied to date, and should indicate how much variation in growth is related to size.

METHODS

External dimensions and weight increase in nestlings of known age were studied on a colony of about 250 pairs of cormorants on Duck Island, Isles of Shoals, New Hampshire (43°, 70° 35′) in the 1971–1972 breeding seasons. Young were individually marked and were weighed every few days with a spring balance. Various external dimensions were measured to the nearest millimeter, as follows. Ulna and tarsus: the greatest length of the segment when the ruler was held parallel to the bone, and with adjacent portions of the appendage held at right angles to that being measured. Culmen: the length from the tip of the bill to the proximal edge of the nostril, with the rule held parallel to the top edge of the lower mandible. Feather lengths (including sheath): the lengths of the third primary inward from the wingtip and one of the central rectrices.

Some nestlings were taken to the Shoals Marine Lab on a nearby island for metabolic studies (to be described elsewhere), then were sacrificed by thoracic compression and frozen, usually well within 10 hours of removal from the colony. Those of unknown age

were weighed and measured as described above, and aged by comparison to known-age young. Internal growth and body components were studied in these frozen specimens.

To minimize loss of blood, dissections were done on partially thawed young, which were subsequently refrozen. Heart, liver and digestive tract were weighed to the nearest 0.1 g on a triple beam balance. Blood was first squeezed from the heart, and the digestive tract included the stomach (emptied) and intestine with all attached organs and membranes.

Specimens were analyzed for water, fat and energy content by methods described in Dunn (1975a). Four samples from each homogenized bird were burned in a Phillipson oxygen microbomb calorimeter. Although the samples bombed constituted only 0.01% to 1.6% of total dry weight (depending on body size), the average deviation from the mean of four determinations of caloric value of lean dry tissue from one specimen was about 10%. The rationale of the method was that a few measurements from each of many birds would give more representative results than would many replications from a few individuals, and the close agreement of results to those of other investigators indicates the validity of this approach.

Although adult males are larger than females, the young are of nearly equal size, so sexes of nestlings cannot be distinguished in the field until near fledging. Sexes were combined in most analyses.

RESULTS

EXTERNAL GROWTH

Average daily weights of cormorant chicks are given in table 1, and conform fairly closely to the logistic equation (fig. 1). Ricklefs (1967a, 1968) developed a method using a constant (K) from fitted growth equations as an index of the rate at which asymptotic weight is being gained. For my cormorant chicks, K was 0.208. This indicates a faster weight gain relative to size than in any other species studied with an asymptotic weight over 500 g, including many altricial and semi-altricial birds as well as generally slower-growing precocial species (Ricklefs 1968, 1973).

Cormorants are also unusual in having an asymptotic weight (1900 g) lower than average adult weight (2047 g; Kury 1968); a situation found as well in the closely related Shag (*Phalacrocorax aristotelis*; Snow 1960). In contrast, other altricial and semi-altricial seabirds reach weights well above adult before fledging (Ricklefs 1973); and the phalacrocoracine pattern is more similar to that of most
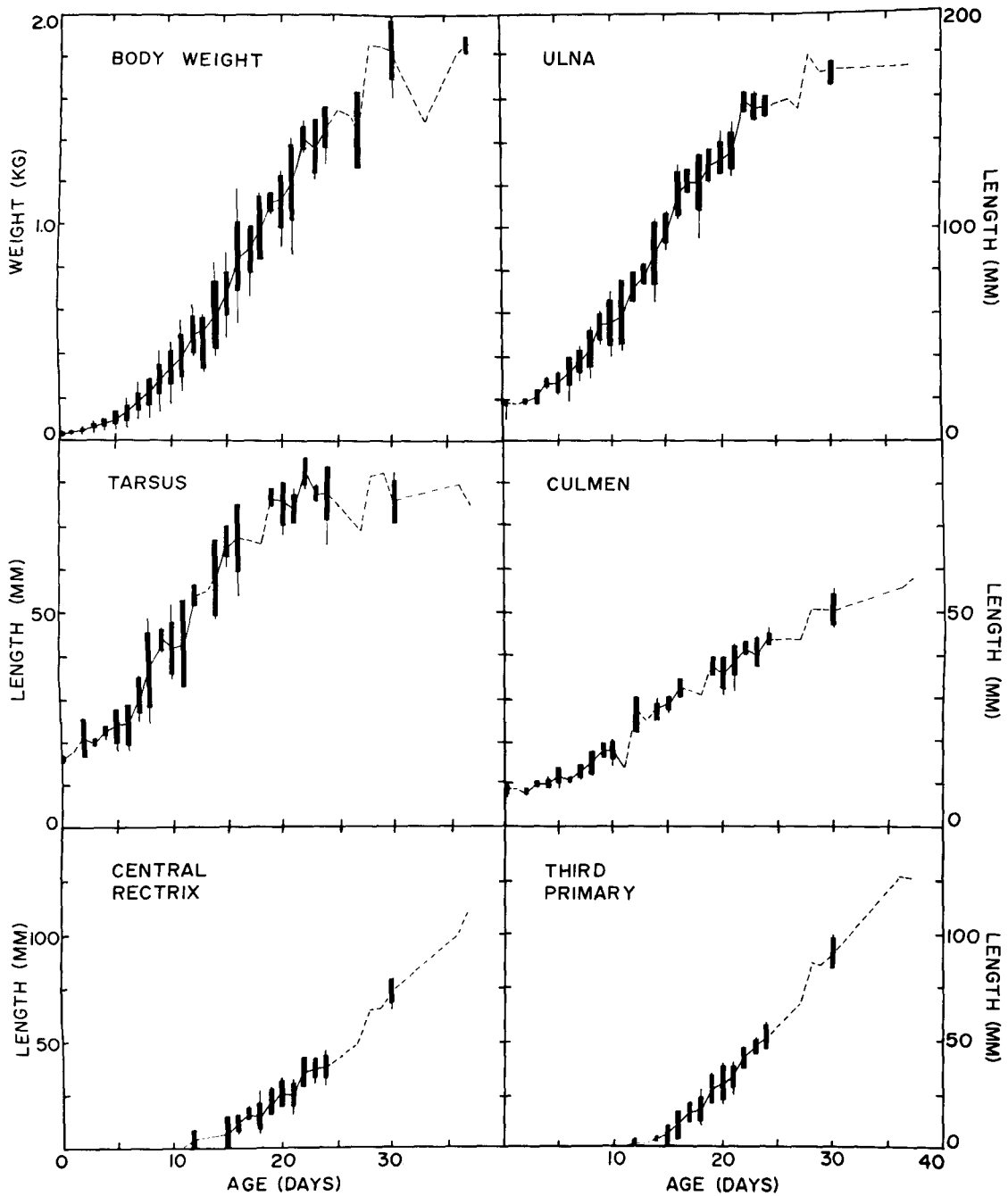
FIGURE 1. Weights and measurements of nestling Double-crested Cormorants. The lines join average daily measurements, and are dotted when connecting to a point representing only one bird. Heavy vertical bars indicate one standard deviation above and below the mean, an d thin vertical lines show the range. Means, deviations and sample sizes are given in Table 1.

passerines. This may be related to the fact that all cormorant chicks are evidently fed by their parents for several weeks after fledging (Snow 1963, Potts 1968), instead of being abandoned at the nest site as is typical of most seabirds with high asymptotic weights (Lack 1968).

External measurements of cormorant chicks are given in table 1 and figure 1. Ulnar length provided the best criterion for aging nestlings, as more growth and less overlap occurred between ages than for any other measurement. Feather lengths were helpful in the older birds. Cormorant hatchlings weighed less than 2% of adult body weight; and tarsus and ulna increased in length by 400% and 820%,

TABLE 1. Weights and measurements of young Double-crested Cormorants.[a]

Age (days)	Weight			Culmen			Tarsus			Ulna			3rd Primary			Central tail feather		
0	34.1 ±	3.5	52	9 ± 1.1		5	16 ± 0.9		5	18 ±	2.2	10	naked					
1	42.9 ±	6.2	23	9		1	18		1	18		1						
2	51.1 ±	8.5	32	9 ± 0.6		3	21 ± 4.7		3	19 ±	0.6	3						
3	69.5 ±	13.0	35	10 ± 0.8		4	20 ± 1.0		4	22 ±	2.9	4						
4	84.4 ±	16.5	26	10 ± 1.0		4	23 ± 1.3		4	28 ±	1.9	5						
5	98.6 ±	23.2	16	12 ± 2.0		6	24 ± 3.8		6	28 ±	4.3	7						
6	135.2 ±	33.5	17	11 ± 0.5		4	24 ± 5.0		4	33 ±	6.4	7						
7	184.1 ±	42.0	18	13 ± 1.7		5	31 ± 4.4		5	38 ±	5.3	6	short down begins					
8	225.5 ±	62.8	11	15 ± 2.8		4	37 ± 8.7		5	43 ±	8.5	6	to grow on body					
9	288.4 ±	72.7	12	18 ± 1.9		5	44 ± 2.3		6	55 ±	4.5	8						
10	343.9 ±	82.1	16	18 ± 2.3		12	42 ± 5.9		10	56 ±	9.7	12						
11	396.5 ±	104.3	6	14		2	43 ± 9.2		2	60 ±	15.5	3	0		1	1		1
12	498.5 ±	75.9	7	28 ± 4.2		2	54 ± 2.8		2	74 ±	7.2	3	2 ± 2.8		2	4 ± 5.7		2
13	447.2 ±	121.9	5	25		1	55		1	79 ±	4.9	2	2		1	dense coat		
14	587.0 ±	157.8	6	27 ± 2.5		3	58 ± 8.2		3	88 ±	14.7	5	4.5 ± 0.7		2	of short black down complete		
15	689.9 ±	104.2	10	29 ± 1.7		5	67 ± 3.6		5	100 ±	6.3	6	6.3 ± 4.7		3	7.0 ± 8.5		2
16	851.0 ±	159.4	10	33 ± 2.3		6	68 ± 7.8		6	116 ±	10.2	8	11.0 ± 6.6		3	11.7 ± 4.5		3
17	893.3 ±	112.0	6							122 ±	5.3	4	17.0 ± 4.8		4	16.5 ± 3.1		4
18	990.0 ±	148.8	9	31		1	66		1	121 ±	12.9	6	17.7 ± 5.8		7	15.4 ± 6.6		7
19	1111.3 ±	45.9	4	38 ± 2.1		2	77 ± 2.1		2	130 ±	7.0	3	27.7 ± 6.4		3	22.3 ± 6.1		3
20	1110.8 ±	118.8	6	36 ± 3.8		4	76 ± 5.0		4	132 ±	7.6	5	30.5 ± 8.4		4	26.0 ± 6.7		4
21	1187.1 ±	189.9	8	39 ± 3.6		7	74 ± 2.6		7	136 ±	8.5	8	33.1 ± 5.0		7	25.4 ± 5.6		7
22	1415.5 ±	64.9	4	42 ± 1.5		3	83 ± 3.5		3	159 ±	4.6	3	42.3 ± 5.5		3	36.0 ± 7.0		3
23	1376.8 ±	129.6	5	41 ± 3.3		4	78 ± 1.7		4	156 ±	6.0	4	47.3 ± 3.6		4	37.5 ± 4.5		4
24	1470.9 ±	102.0	7	44 ± 1.5		6	78 ± 6.3		6	157 ±	5.0	6	51.7 ± 5.7		6	37.8 ± 5.3		6
25	1550.0		1															
26	1540.0		1							160		1						
27	1462.5 ±	180.3	2	44		1	69		1	155		1	66		1	49		1
28	1850.0		1	51		1	82		1	180		1	87		1	65		1
29	1850.0		1	51		1	83		1	172		1	85		1	65		1
30	1833.8 ±	143.6	4	51 ± 3.8		4	76 ± 5.2		4	172 ±	4.4	4	91.3 ± 7.1		4	73.3 ± 5.7		4
33	1500.0		1															
36	1810.4		1	56		1	80		1	174		1	127		1	99		1
37	1847.2 ±	46.4	2	58		1	75		1	174		1	126		1	110		1

[a] Measurements fluctuate as different birds were measured at each age.

respectively, between hatching and fledging. Most smaller altricial birds have measurements at hatching closer to those of adults (Dunn 1973), which is probably related to the larger egg (relative to body size) laid by smaller birds (Lack 1968). In relation to the rate of increase in body weight, tarsal growth in cormorants slowed after the first week; while bill and particularly ulna grew more rapidly later in the nestling period than in the first week. Differences in the rate of growth among tarsus, bill etc. have also been noted in other birds (Siegfried 1966, Karhu 1973), and the subject deserves more study.

INTERNAL GROWTH

The weights and measurements of various internal organs throughout growth are given in fig. 2. In nestlings removed from heavily pipped eggs, yolk constituted about 16% of body weight. This is very high for an altricial species, but is in line with Schmekel's (1961)

data showing that larger birds hatch with a higher proportion of yolk than small ones. Some of this yolk would probably be used up during the completion of hatching. Any remaining reserves must be absorbed rapidly, as they made up less than 1% of body weight at 2 days of age.

Internal organ growth followed a sigmoid pattern, but not necessarily in parallel with weight increase (fig. 1). The digestive system grew particularly rapidly, as illustrated by the increase in intestine length. This tripled in the first week, then doubled again slowly over the next 30 days.

BODY COMPOSITION

Fat and water ratios (water or fat content divided by lean dry weight) are shown in figure 3. Water ratios declined from about 7 to 2, the range and rate of decrease being very similar to those found for other altricial species (Ricklefs 1967b, 1974). Brisbin 1969,
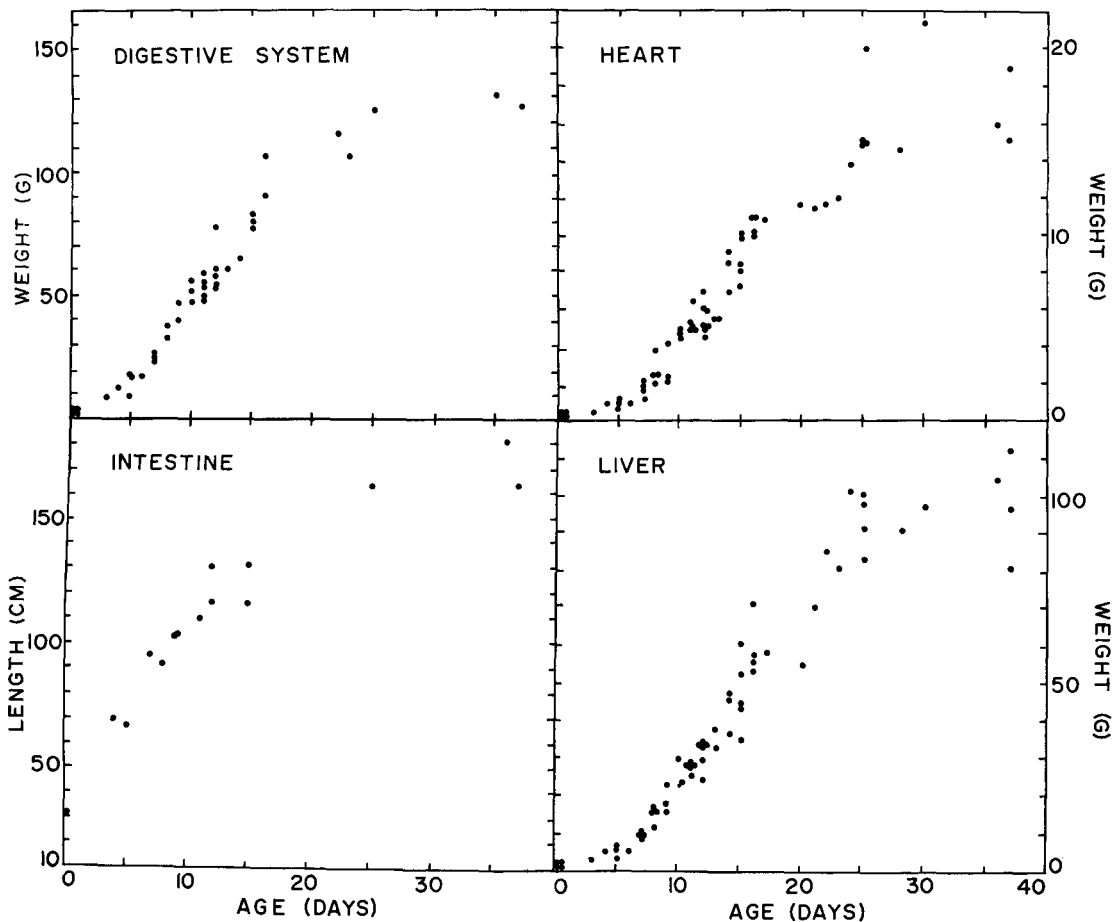
FIGURE 2. Weights and measurements of internal organs of nestling Double-crested Cormorants. Each point represents the measurement for a single bird.

Skar et al. 1972, Westerterp 1973). This decline represented a drop in water content from about 85% to 65% of body weight (fig. 4). Water ratio decreased for females somewhat faster than for males, perhaps because the larger males require a longer time to reach adult size. Precocial and semi-precocial chicks hatch with a lower proportion of water than altricial young, but also show gradual decreases during growth (Brisbin 1965, Norton 1970, Brisbin and Tally 1973, Ricklefs pers. comm.).

The high fat ratios of hatchling cormorants (fig. 3-B) resulted from the large amounts of remaining yolk, and dropped as the yolk was consumed. Thereafter, fat ratios increased through the nestling period, indicating that fat levels increased more rapidly than lean dry weight (fig. 4).

Fat ratios also rise with age in nestling Barn swallows (*Hirundo rustica*; Ricklefs 1967b), and probably do so in Ring Doves (*Streptopelia risoria*; Brisbin 1969). Although Brisbin reported no rise in fat ratios, he measured no

birds between ages 1 and 8 days. Nestlings with yolk may have been included in the first sample, while nestlings of the age to have low fat ratios would not have been sampled. Other species, however, appear to have no rise in fat ratio with growth (Redwinged Blackbird, *Agelaius phoeniceus*; Ricklefs 1967b and Cactus Wren, *Campylorhynchus brunneicapillus*; Ricklefs 1975). These species do increase their fat levels, but at a rate similar to the rise in lean dry weight.

The results of calorimetry of nestlings are shown in figure 5. Energy content of dried tissue (part A) rose through growth because of increased fat content. The slightly faster rise in females was significantly different from that in males ($p < 0.01$). Lean dry energy content (fig. 5-B) did not change significantly with nestling age, and averaged 4.99 kcal/g; a value in close agreement with results for various other birds (Ricklefs 1974).

Average live weight caloric density (the line in fig. 5-C) was calculated from the regression in part A (for 22 samples) and from a regres-
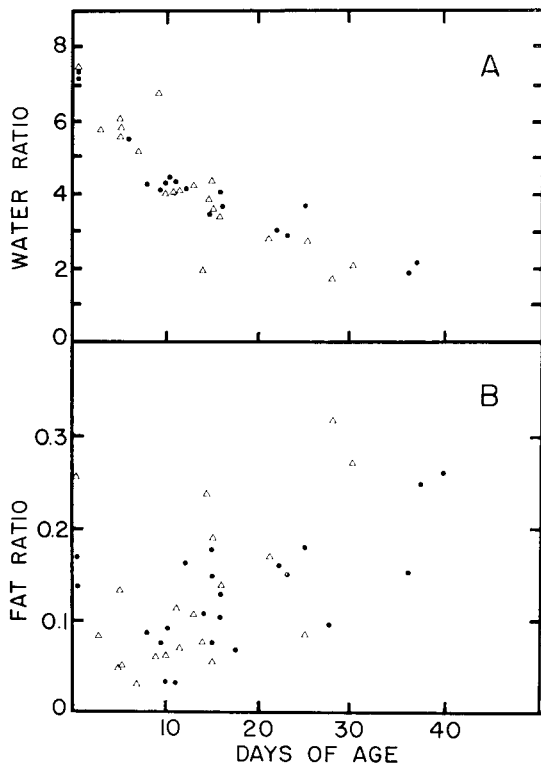
FIGURE 3. Water (A) and fat (B) ratios of nestling Double-crested Cormorants. Each point represents the water or fat content of one bird divided by its lean dry weight. Males are shown by circles, females by triangles.

FIGURE 4. Proportional body composition of nestling Double-crested Cormorants throughout growth. Percentages are cumulative.

sion of water content on age which included data for 37 birds. The points in part C represent the smaller number of individuals for which both water and caloric determinations were made. The solid line thus gives the average for a large group of birds, including many females (which have higher caloric densities than males during the latter stages of growth), and should better represent the average condition than the few points for males alone.

The dotted line in fig. 5-C indicates my estimate of caloric density in older nestlings, and was derived as follows. Adult live weight caloric densities for a large number of birds range from about 1.8 to 2.6 kcal/g, depending largely on fat content (Yarbrough and Johnson 1965, Zimmerman 1965, Cummins and Wuycheck 1971, Skar et al. 1972). Rapid increase in nestling caloric density apparently ends abruptly around fledging age (Skar et al. 1972, Ricklefs 1975). As the maximum average caloric density of cormorant chicks is likely to be somewhat higher than the highest value measured directly (about 2 kcal/g, fig. 5-C), because that figure was for males with
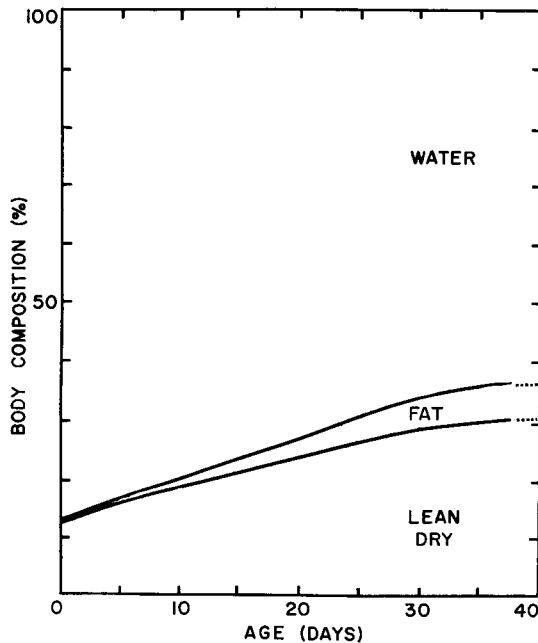
lower caloric density than females, I assumed that caloric density levels off at about 2.2 kcal/g live weight.

Live weight caloric density of cormorant chicks rose from about 0.65 kcal/g at 2 days of age (after yolk absorption) to about 2.2 kcal/g near fledging age. The change was nearly linear, and parallels closely the values estimated for Barn Swallows (Ricklefs 1967b). Figures for the Ring Dove (Brisbin 1969) range from about 1.0 to 2.2 kcal/g, but may have included hatchlings containing significant amounts of yolk. Kale (1965), Skar et al. (1972) and Westerterp (1973) showed narrower ranges (0.8 to 1.8 kcal/g for nestling Long-billed Marsh Wrens, *Telmatodytes palustris*; 0.7 to 1.7 for nestling Meadow Pipits, *Anthus pratensis*; and 0.9 to 1.8 kcal/g for young Starlings, *Sturnus vulgaris*, respectively). The first two authors averaged results for differently aged young, however, and the real ranges were probably broader. Further variation in results may be related to the variance in stage of maturity at fledging in different species.

DISCUSSION

BODY COMPOSITION

The similarity of water ratios among altricial species of very different size and habit suggests that the decline in the proportion of body water is a developmental process little affected
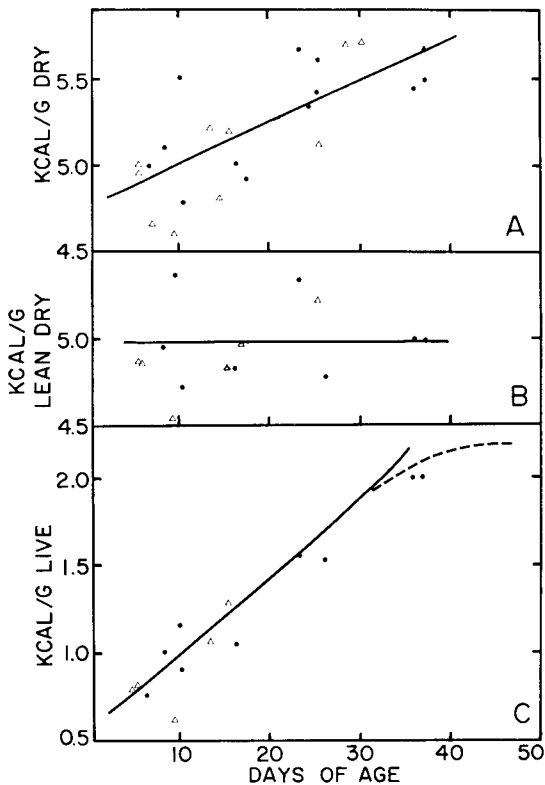
FIGURE 5. Energy content of nestling Double-crested Cormorants. Points in Part A represent average kcal/g dry weight from 4 determinations for each bird. The slope of the regression equation ($Y = 4.78 + 0.024X$) is significantly different from 0 ($p < 0.001$). $r^2 = 0.55$ for both sexes. Part B shows energy content of lean dry tissue (the same results as in Part A, after subtraction of 9.0 kcal/g of fat). The line in Part B shows the average energy value of 4.99 kcal/g lean dry tissue. Part C gives average energy content of fresh tissue (see text for explanation). In all parts, males are represented by circles, females by triangles.

by amount of weight gain or by differing ecological requirements. Fat levels appear more variable, however, and have been shown to depend to some extent on feeding conditions (Brenner 1964), particularly in precocial chicks (Norton 1970).

Brisbin and Tally (1973) suggested that with enough study, predictive models of caloric value could be constructed, obviating the need for tedious analysis of every species. Many investigators could use such estimates, as in calculating energy required for growth and in analyzing selection for growth pattern, optimal parental feeding rates and optimal brood size. As the ranges and rate of change in kcal/g live weight appear to be similar for a number of altricial young of different body size and ecological requirement, it now appears justifiable to use a linearly increasing caloric density, from about 0.7 kcal/g at hatch-

ing to about 2.0 kcal/g at fledging age, for any altricial species.

Estimation of live weight caloric density for precocial and semi-precocial chicks, on the other hand, is as yet unjustified. These birds have energy contents at hatching close to those of adults (Cummins and Wuycheck 1971), but large variation in fat content, and thus live caloric value, can occur (Brisbin 1965, Norton 1970, Koelink 1972, Brisbin and Tally 1973). Analysis of the proportions of water, fat and lean dry tissue should, however, be sufficient for estimation of energy content throughout growth, as the caloric values of these components are fairly constant (Ricklefs 1974).

ORGAN GROWTH

Recent analyses of avian development have compared species on rate of weight gain, increase in external dimensions and attainment of thermoregulation (Ricklefs 1968 and 1973, Dunn 1973 and 1975b, respectively). In addition, Ricklefs (1967b) presented some data comparing the growth of internal organs in altricial and precocial birds. Table 2 extends his analysis with the addition of more data.

The relative growth constant represents b in the formula $W_o = aW^b$, where W_o is the weight of the organ, W is body weight, and a and b are constants. The value most easily measured is b, which is the slope of the log-log plot of organ weight on body weight, and represents growth faster or slower than body growth as a whole when b has a value of greater or less than 1.0, respectively (Ricklefs 1967b).

Growth of the digestive system is initially very rapid in the altricial and semi-precocial birds shown in table 2, slowing in later stages. Initial enlargement allows nestlings to process large amounts of food relative to body size, presumably contributing to the high growth rates seen in most altricial and semi-precocial birds (Ricklefs 1968 and 1973). Bee-eaters show a decrease in gizzard weight near fledging, apparently as a result of a switch in food items (Fry 1972). The digestive system of precocial domestic chicks grows more slowly after hatching than in altricial species.

Liver and heart are thermogenic, and it might be expected that a greater proportion of growth of these organs should occur in the egg in species that can thermoregulate soon after hatching. This is borne out in the data for the chicken (table 2), but data for the Herring Gull (*Larus argentatus*; which also thermoregulates soon after hatching, unpubl. data) indicate that its internal growth pattern

TABLE 2. Relative growth constants of internal organs of nestling birds.

Species	Relative growth constant of:[1]			Source
	digestive tract	liver	heart	
ALTRICIAL SPECIES				
Double-crested Cormorant,	1.20(1–5)[b]	1.20 (1–8)	1.40 (0–8)	this paper
Phalacrocorax auritus	0.62(6–35)	0.82 (9–35)	0.85 (9–35)	
Domestic Pigeon,	1.20(0–5)[b]	1.60 (1–3)	1.80 (0–3)	Brody 1945 and
Columba livia	1.00(6–7)	1.10 (4–9)	1.04 (4–9)	Kaufman 1962
		0.40(10–12)	0.75(10–12)	
Red-winged Blackbird,	1.15(0–3)[c]	1.64 (0–3)	1.03 (0–12)	Ricklefs 1967b
Agelaius phoeniceus	0.22(4–12)	0.94 (4–12)		
Starling,		1.95 (7–9)		Portmann 1938
Sturnus vulgaris		0.34(10–12)		
		–0.35(13–17)		
Cactus Wren,	0.73(0–8)[c]	1.21 (0–19)	0.62 (0–7)	Ricklefs 1975
Campylorhynchus				
brunneicapillus	0.00(9+)		1.22 (8+)	
Red-throated Bee-eater,	1.35(4–7)[d]	2.81 (4–7)		Fry 1972
Merops bulocki	–0.60(8–18)	1.12 (8–21)		
Vesper Sparrow,		1.2	1.1	Dawson and
Pooecetes gramineus				Evans 1960
SEMI-PRECOCIAL SPECIES				
Herring Gull,	0.84(3–33)[b]	1.20 (3–<12)	1.0 (3–<12)	Dunn unpubl.
Larus argentatus		0.82(<12–33)	0.65(<12–33)	
PRECOCIAL SPECIES				
Domestic Fowl Gallus	0.30[d]	0.44	0.20	Brody 1945 and
gallus, var. domesticus	0.48	0.67		Latimer 1924

[a] See text for explanation of relative growth constants. The figures in parentheses refer to the ages in days to which the growth constants apply.
[b] Emptied stomach, and intestines with attached membranes and organs.
[c] Stomach only.
[d] Gizzard only.

is more typical of altricial than of precocial species. (The same is true in certain tern species; Ricklefs pers. comm.) Growth of skeletal muscle should show better correlations to thermoregulation, while the growth of heart and liver must depend mainly on other factors.

More data on internal organ growth of precocial and semi-precocial species should help clarify the patterns of internal development and the reasons for the differences among developmental modes.

SUMMARY

Development of altricial Double-crested Cormorant nestlings involved changes in weight gain, external dimensions, organ weight, body composition and caloric density; and the normal pattern of growth is described here in detail.

Weight gain was unusually rapid for a large bird, and leveled off below adult weight. External dimensions grew in length proportionally more than in smaller species. As is typical of small altricial birds, the internal organs of cormorants grew more rapidly than the body as a whole in the early stages of the nestling period.

Water content of tissue declined through the growth period as in other altricial birds, but fat content increased more in the cormorant. Live weight caloric density increased linearly from about 0.65 kcal/g to about 2.2 kcal/g.

Live weight caloric density for any altricial species can be estimated as rising from 0.7 kcal/g at hatching to about 2.0 kcal/g at fledging. Compositional analysis is required for caloric estimations in precocial and semi-precocial species, however.

Comparisons of organ growth showed that precocial birds hatch at a more completely developed stage than altricial and semi-precocial species.

ACKNOWLEDGEMENTS

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