

# POSTNATAL DEVELOPMENT OF LEACH'S STORM-PETREL<sup>1</sup>

ROBERT E. RICKLEFS, SUSAN WHITE,<sup>2</sup> AND JOHN CULLEN<sup>3</sup>

*Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA*

**ABSTRACT.**—Thirty-one nestling and 2 adult Leach's Storm-Petrels were collected on Kent Island, New Brunswick. The ages of the nestlings were estimated by comparing weights and wing lengths to those of chicks of known age obtained by other investigators on Kent Island. The specimens were dissected into 10 components for each of which we determined the water, lipid, ash, and nonlipid ash-free dry contents. The body proportions of the petrel neonate are similar to those of the neonates of starlings, terns, and quail. Water levels in the tissues are consistent with precocial development. The size of the neonate relative to that of the adult is large (16%) compared to other species, and the postnatal growth increments of body components (ratio of adult to neonate) are correspondingly small, ranging from ratios of between 3 and 4 for the viscera, head, and legs, to 8 for the integument, 14 for the wings, and 59 for the pectoral muscles.

The pectoral muscles increase to 5% of body weight within 10 days, after which they apparently play a major role in heat production. Correlated with their early maturation, as indicated by decrease in water content, the pectoral muscles grow slowly throughout the latter part of the postnatal development period. Their growth rate at that time may constrain the overall rate of growth of the chick.

Our results suggest, first, that with respect to many aspects of development petrels resemble semi-precocial species more closely than semi-altricial species (as defined by Nice). Second, the slow growth of petrels is consistent with their precocious mode of development; explanations based upon reduced energy requirements of slowly growing chicks (cf. Lack) are not required. *Received 4 September 1979, accepted 31 March 1980.*

THE Procellariiformes are a varied group of pelagic seabirds that breed on remote islands or in other inaccessible places. Most of the small species dig burrows for nesting, all lay a single large egg, and many species have prolonged periods of incubation and development. In addition, nestlings of most procellariiform birds accumulate large amounts of fat, which diminish before fledging. Lack (1968) described the unique features of clutch size and development in the Procellariiformes as adaptations to the food supply. Adult albatrosses, shearwaters, and storm-petrels forage at great distance from the breeding colony and return infrequently to feed the young. Food supplies are thought to be variable and their availability greatly affected by weather. The one-egg clutch of all Procellariiformes, indeed of most pelagic seabirds, suggests adaptation to minimize the food required by the brood. Lack suggested that slower growth may further reduce food requirement and allow procellariiform birds to exploit more distant or sparse food resources. Fat stores presumably enable chicks to survive occasional long intervals between visits from their parents.

In comparisons among birds of diverse orders, variation in growth rate has been related to adult body size and to the precocity of the chick at hatching: chicks of larger species tend to grow more slowly than those of smaller species (Lack 1968, Ricklefs 1968); chicks that are self-sufficient (precocial) at hatching grow much more

---

<sup>1</sup> Contribution Number 46 from the Bowdoin Scientific Station.

<sup>2</sup> Present address: 540 Robin Hill Circle, Brandon, Florida 33511 USA.

<sup>3</sup> Present address: Department of Pathology, School of Veterinary Medicine, University of California, Davis, California 95616 USA.

TABLE 1. Relative size and water indices of organs in one neonate and two adult Leach's Storm-Petrels, and growth increment and allometric constants of these components.

Component	Percentage nonlipid weight				Water index		Growth increment		Allometric constant (b) <sup>c</sup>
	Wet		Dry		Neonate	Adult	Ratio <sup>a</sup>	Log <sub>e</sub> <sup>b</sup>	
	Neonate	Adult	Neonate	Adult					
Integument	15.4	23.0	23.5	38.1	2.4	0.5	8.1	2.1	1.28
Body	35.7	26.1	34.8	19.9	4.3	2.3	4.0	1.4	0.84
Stomach	4.3	2.9	2.9	1.5	6.7	3.7	3.6	1.3	0.85
Intestine	6.1	3.2	4.2	1.8	6.5	3.5	2.8	1.0	— <sup>d</sup>
Heart	1.5	1.7	0.9	1.0	— <sup>e</sup>	3.1	6.2	1.8	0.86
Liver	5.4	4.4	4.8	3.3	4.8	2.4	4.5	1.5	1.00
Head	16.0	11.3	12.6	7.9	5.5	2.6	3.8	1.3	0.70
Legs	11.7	7.5	13.3	7.3	3.5	1.6	3.5	1.2	0.73
Pectoral muscles	1.2	13.4	0.6	9.4	— <sup>e</sup>	2.6	59.0	4.1	1.96
Wings	2.6	6.6	2.3	9.7	4.9	0.7	13.7	2.6	1.52
Total	—	—	—	—	4.1	1.5	5.4	1.7	

<sup>a</sup> Ratio of the mass of the adult component ( $n = 2$ ) to that of the neonate ( $n = 1$ ), based on nonlipid wet masses.

<sup>b</sup> Natural logarithm of the growth increment.

<sup>c</sup>  $b$  is the exponent in the equation  $Y = aX^b$  relating component mass  $Y$  to total mass  $X$ , based on nonlipid wet masses; based on 31 chicks and 2 adults.

<sup>d</sup> Component extremely variable.

<sup>e</sup> Components were too small to estimate water content accurately.

slowly than chicks that are dependent (altricial) (Ricklefs 1973; 1979a, b). As in precocial and semi-precocial species, procellariiform neonates have a thick down and are thermally independent at an early age. But because their eyes are closed and they do not leave the nest, Nice (1962) tentatively classified them as semi-altricial. She noted, however, that the relative sizes of their egg yolks were more consistent with those of semi-precocial species. If procellariiformes were semi-altricial, their potential growth rates presumably would be comparable to those of species in groups having altricial or semi-altricial development (songbirds, raptors, doves, herons, cormorants, etc.), and their realized (= slow) growth rates could be limited by rate of feeding. If the growth rate of procellariiform chicks were limited by availability of energy or nutrients, it should be possible to demonstrate that their food requirements are reduced relative to the requirements of more rapidly growing altricial and semi-altricial species. With this goal in mind, we initiated a study of development in Leach's Storm-Petrel (*Oceanodroma leucorhoa*) in New Brunswick, Canada. This paper describes postnatal growth. Elsewhere (Ricklefs et al. 1980) we consider energetics, and subsequent papers will cover feeding, fasting, and embryonic development.

Leach's Storm-Petrel (family Hydrobatidae) has an extensive breeding distribution in the North Atlantic and North Pacific oceans (Palmer 1962). The North Atlantic subspecies is *O. l. leucorhoa*. Its breeding in eastern North America has been described by Bent (1922), Gross (1935), Palmer (1962), and Wilbur (1969). Other studies have been published by Ainslie and Atkinson (1937) and Ainley et al. (1975). The most complete general account is that of Palmer (1962), who summarized many of the unpublished findings of C. E. Huntington on Kent Island, New Brunswick.

#### METHODS

The study described in this paper was conducted at the Bowdoin Scientific Station on Kent Island, New Brunswick between 24 and 38 July and between 1 and 8 September 1972. We collected 31 chicks

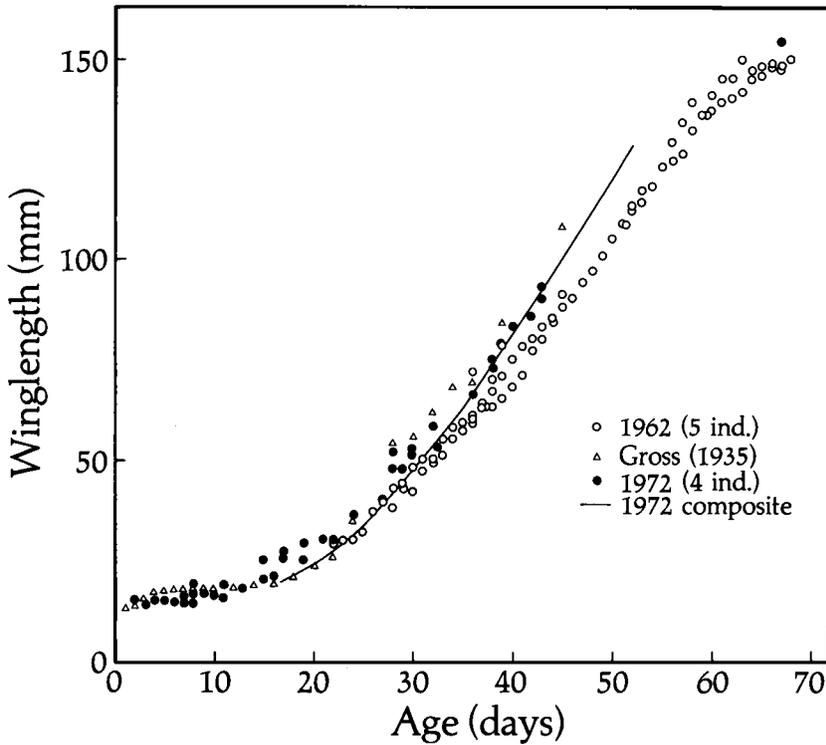


Fig. 1. Relationship between wing length and age based on Gross (1935) and unpublished data of C. E. Huntington (1962) and J. McEnroe (1972). The solid line was estimated from growth increments of 13 chicks over 5-day intervals (see text). Day of hatching = 1.

and 2 adults. The specimens were frozen and processed later according to the methods of Ricklefs (1975). Briefly, thawed specimens were measured and then dissected into 10 components: integument (skin and feathers, including subcutaneous fat), stomach (contents removed), intestines (contents not removed), heart, liver, head, legs, wings, pectoral muscles, and body (carcass). Each component was dried to constant mass at 40–45°C under vacuum, extracted in a 5:1 mixture of petroleum ether and chloroform, which removes both triglycerides (storage lipids) and phospholipids (structural lipids), and ashed in a muffle furnace at 550°C. The primary data for each component were the masses of the wet, dry, nonlipid (= lean) dry, and ash components. From these we calculated the following: water = wet - dry; lipid = dry - nonlipid dry; nonlipid wet = wet - lipid; water index = water/nonlipid dry. The amount of mineralized bone was estimated by the expression bone = ash - (water × 0.02), in which the subtracted quantity represents approximately the level of dissolved ions (g ash/g water) in tissues lacking bone (Ricklefs unpubl.).

We estimated allometric constants ( $b$ ) relating component mass ( $Y$ ) to total mass ( $X$ ) by least squares fitting of  $a$  and  $b$  in the equation,  $\log Y = \log a + b \log X$ . We used the graphical method of Ricklefs (1967a) to fit Gompertz equations, having the form

$$M(t) = A \exp(-\exp[-K(t - t_i)]),$$

to curves relating mass [ $M(t)$ ] to age  $t$ . The constant  $t_i$  is the age at the point of inflection (maximum growth rate),  $K$  is the growth rate constant, and  $A$  is the asymptote or mass plateau. We determined that the Gompertz equation gave a better fit to the data than either the logistic or von Bertalanffy equations (see Ricklefs 1967a).

Ages of chicks were assigned by criteria derived from unpublished measurements of mass and wing length obtained by C. E. Huntington and J. McEnroe on Kent Island. Details are given in the results section.

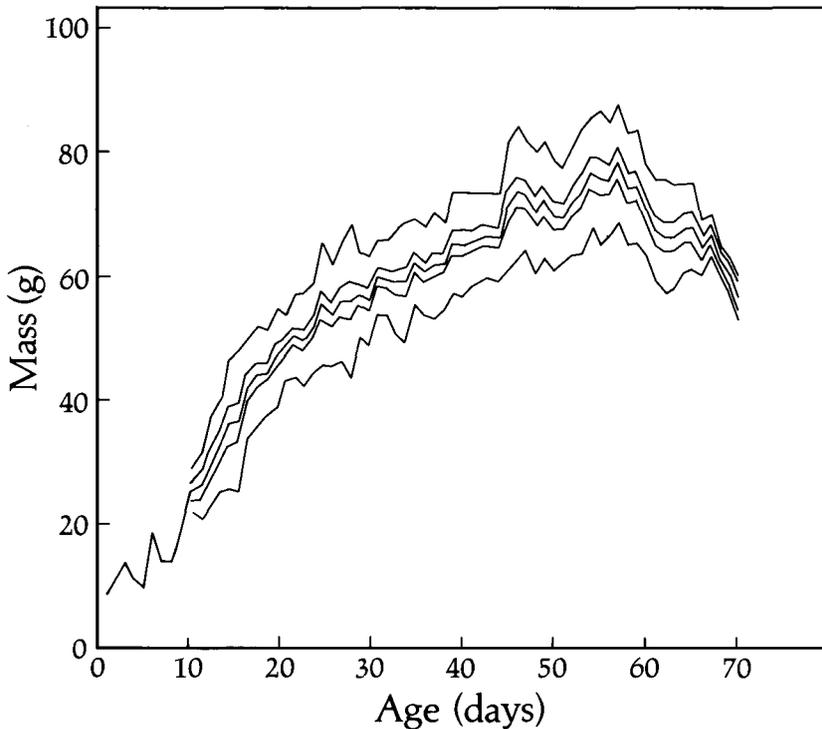


Fig. 2. Relationship between mass and age based on 19 chicks weighed by C. E. Huntington on Kent Island in 1962. The lines bounding the mean are  $\pm 1$  standard error and  $\pm 1$  standard deviation. Sample sizes varied between 1 and 2 for days 1-9, 6 and 11 for days 10-14, 12 and 19 for days 15-62, and less than 10 for days 63-69.

## RESULTS

*General biology.*—Adult petrels have a mass of about 45 g (Palmer 1962). The average mass of 45 partially incubated eggs on Kent Island, New Brunswick was 8.8 g (Gross 1935). Thirty-three relatively fresh eggs (spec. grav.  $\geq 1.0$ ), weighed on Baccalieu Island, Newfoundland on 10 and 12 June 1978, had an average mass of 10.7 g (SD = 1.0 g and SE = 0.2 g) (W. A. Montevecchi pers. comm.). The egg hatches after between 38 and 46 days ( $\bar{x} = 42.4$ , SD = 2.2,  $n = 14$ ; C. E. Huntington pers. comm.), and the chick leaves the nest 63-70 days after hatching (C. E. Huntington in Palmer 1962).

The eyes of the neonates are closed. At hatching, the chicks are covered with a thick down (protophile plumage). A second (mesophile) down begins to grow during the second week, and adult-type (teleophile) feathers appear during the fourth week in most feather tracts (Palmer 1962). The young are brooded less than 5 days. The eyes usually open before the end of the second week after hatching.

*Adult-neonate comparison.*—We collected only one neonate. This bird is compared to two adults in Table 1. Although it is precarious to base comparisons on so few individuals, the amount of variation among both neonates and adults of other species (e.g. Ricklefs 1979a) is small, and confidence limits on estimates of parameters typically are narrow, particularly compared to differences among species. From

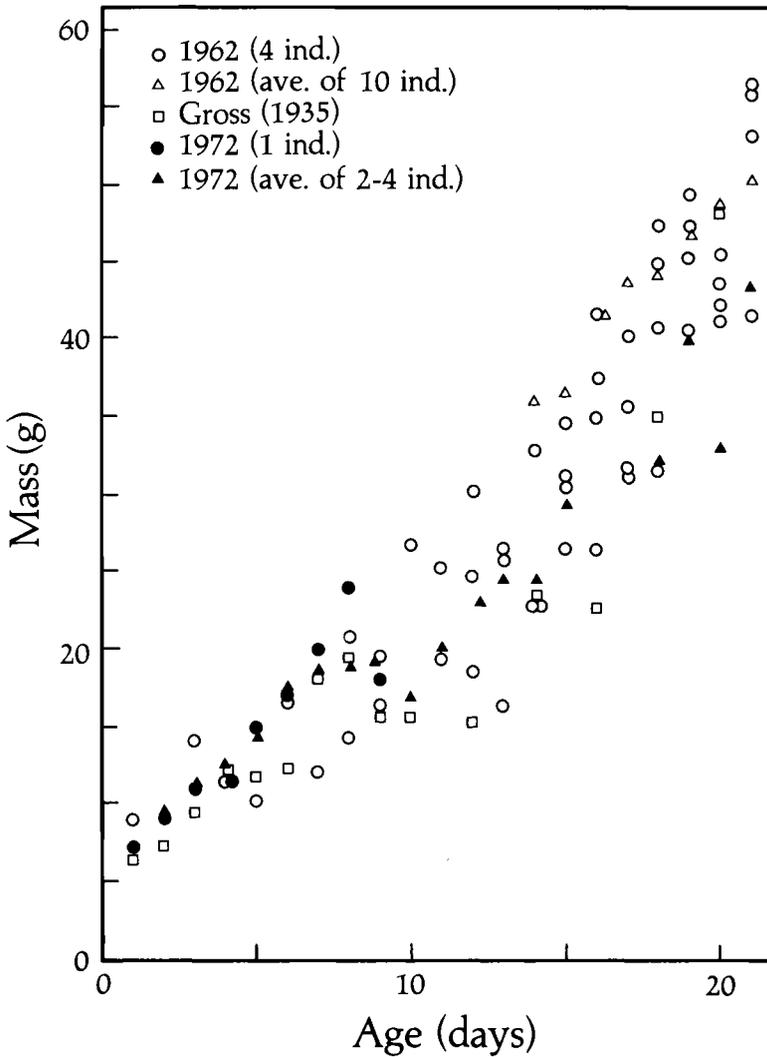


Fig. 3. Relationship between mass and age during the first 3 weeks after hatching, based on Gross (1935) and unpublished data of C. E. Huntington and J. McEnroe.

nest checks, we determined that the neonate was less than 24 h old. It had a small amount of yolk in its gut and its mass (7.05 g) was consistent with the hatching mass expected according to the average size of eggs in the population. Six neonates weighed by J. McEnroe in 1972 had an average mass of 7.3 g. The sex and breeding status of the two adults were not determined. Their masses were 37 and 44 g.

The growth increment (ratio of the mass of a component of the adult to that of the neonate), natural logarithm of the growth increment, and the allometric growth constant ( $b$ ) of each organ or component are also presented in Table 1. These values parallel the change in proportions of each component between hatching and adulthood. In general, if the growth increment of a component exceeds that for the individual as a whole (ratio = 5.4), its relative proportion increases during devel-

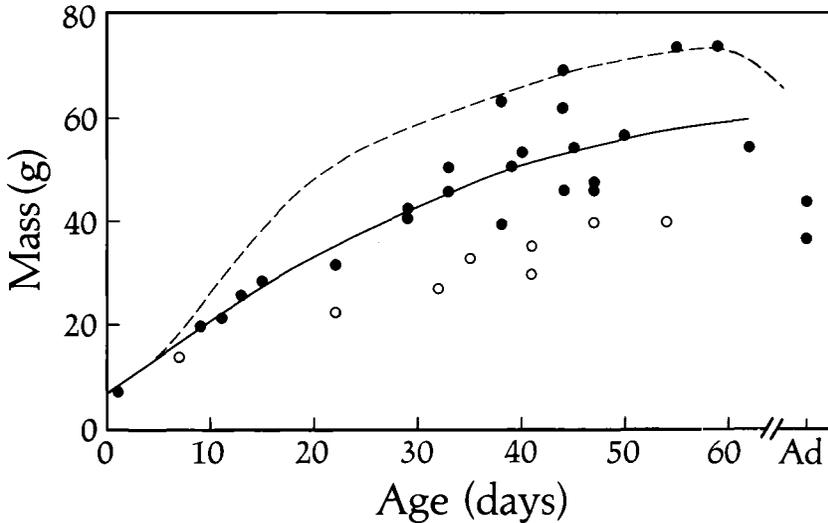


Fig. 4. Relationship between mass and estimated age for the specimens collected in this study. These are compared with the general trend of the average values of Huntington's data from 1962 (dashed line). Eight chicks were kept without food for periods up to a week. These birds (open circles) are excluded from some of the analyses in this study and will be discussed in more detail elsewhere. Solid line drawn by eye to suggest the trend.

opment, and its allometric constant is greater than 1. Some minor discrepancies in these values, e.g. for the heart and liver, appear when allometric constants are based on smaller chicks only, owing to variation among larger chicks, or when the growth is not strictly allometric.

*Increase in mass and wing length: aging criteria.*—Gross (1935) tabulated masses and measurements of an unspecified number of petrel chicks on Kent Island. Mass increased, with considerable variability about the trend, to a maximum of almost 70 g by 5 weeks of age. Ricklefs (1973) fitted Gross's data by a Gompertz equation having asymptote ( $A$ ) = 75 g and growth rate ( $K$ ) =  $0.074 \text{ days}^{-1}$ . Gross's table of measurements indicated that the lengths of appendages increased little during the first 2 weeks, while mass at least tripled to 23 g. During the third week, the wing and feathers began to grow rapidly.

Figure 1 summarizes the increase in wing length (chord of folded wing, Baldwin et al. 1931) with age, including data for the chick or chicks measured by Gross (1935), 5 chicks of known age measured by C. E. Huntington in 1962, and 4 chicks of known age measured by J. McEnroe in 1972. In addition, we have plotted a composite curve based on 13 5-day growth increments obtained during our study (see Ricklefs and White 1975, 1978).

Figure 2 presents unpublished masses obtained by C. E. Huntington from 19 chicks in 1962. Masses of chicks studied by McEnroe in 1972 were consistently below the 1962 average after the third week of age. Figure 3 summarizes all the available masses for chicks during the first 3 weeks after hatching. Although masses vary greatly according to the history of feeding of each chick and the length of time since its last feeding (e.g. Harper 1976), they allow one to estimate the age of the chick during the first 3 weeks as reliably as do lengths of feathers or appendages.

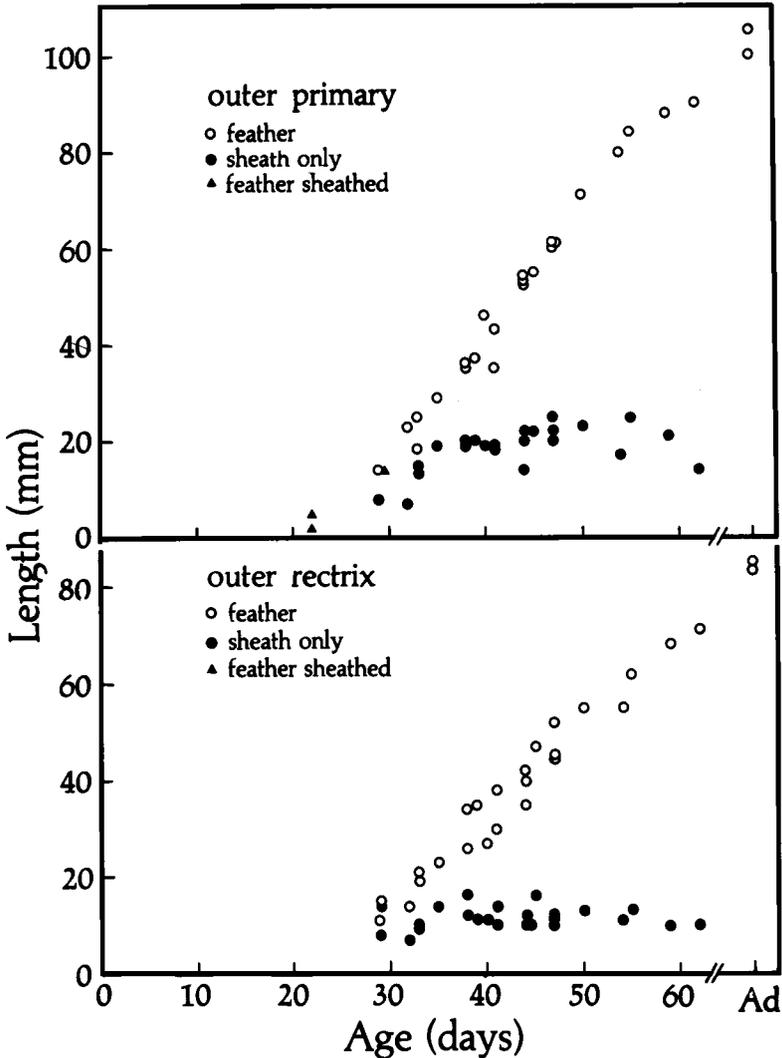


Fig. 5. Relationship between estimated age and the lengths of the outer primary, outer rectrix, and their sheaths.

After the third week, we used only wing length (Fig. 1) to estimate age. We feel that most of our estimates of age are within  $\pm 3$  days of the true chronological age and that the estimates are unbiased.

In Fig. 4, masses and estimated ages of specimens collected in this study are compared to the growth curve obtained in 1962 (Fig. 2). Although the 1972 chicks generally had less mass than the average for 1962, all had large quantities of fat (Ricklefs et al. 1980). Furthermore, in order to measure their metabolic rates, most of the chicks were kept in the laboratory for a day or more before they were sacrificed. Masses reported here follow whatever loss occurred during captivity. High fat levels in our specimens and the fact that, in 1972, growth increments in the length of the wing were similar to those reported by Gross and Huntington indicate that

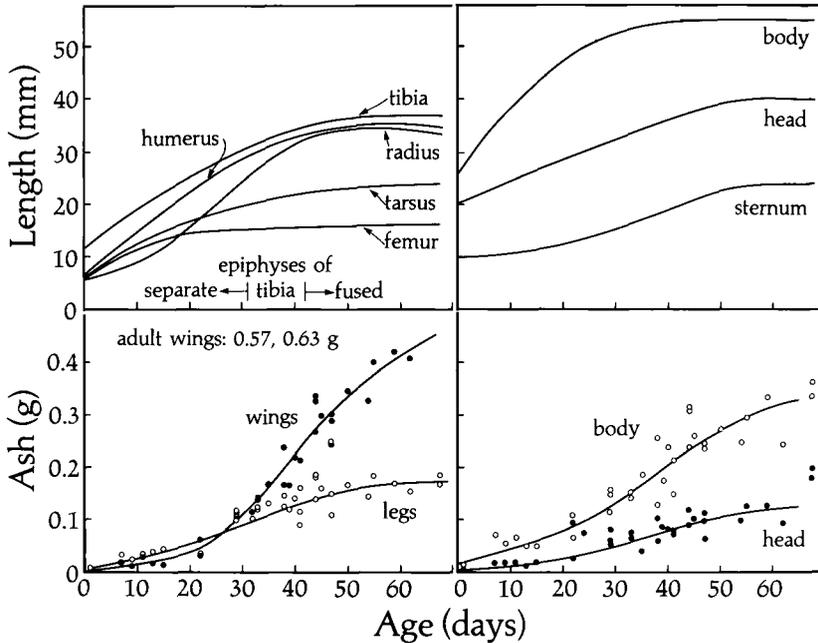


Fig. 6. Relationship between estimated age and the lengths of several bones and ossification of bones. Ash deposited in bone was estimated as total ash -  $0.02 \times$  water (see text). Variability of data is similar to that in the lower graphs. Curves were drawn by eye.

development rates of the chicks in our sample were not adversely affected by poor nutrition.

*External measurements.*—Our data on the lengths of the tarsus, culmen, fifth and outer primaries, and outer rectrix are consistent with Gross's measurements. The tarsus and culmen are approximately one-third and one-half adult length at hatching and complete most of their growth within 4 weeks. The primaries and rectrices begin to grow at about 3 weeks (Fig. 5).

*Bone development.*—We measured the lengths of bones in the ashed remains of the wings (humerus and radius), legs (femur, tibia, and tarsus), body (sternum and fused vertebral column), and head (tip of beak to posterior edge of skull). Although weakly ossified bones tend to shrink during ashing, the measurements nonetheless present a general picture of skeletal growth (Fig. 6). In the leg, the femur is fully grown by 20 days, whereas the tibia and tarsus continue to grow until between 40 and 50 days, the age at which growth of the humerus and radius ceases. The epiphyses of the tibia were separated in all birds younger than 31 days and fused in all birds older than 42 days. In the legs, mineralization appears to proceed gradually and continuously and is completed before fledging. In the wings, mineralization does not begin until about 3 weeks and achieves only two-thirds adult level by 60 days.

Measurements of the axial skeleton are variable but suggest completion of growth of the fused vertebral column by 20 days and of the head and sternum by 40 days. Mineralization of the body skeleton parallels that of the legs and is nearly completed by fledging. Mineralization of the head follows the same general time course as the

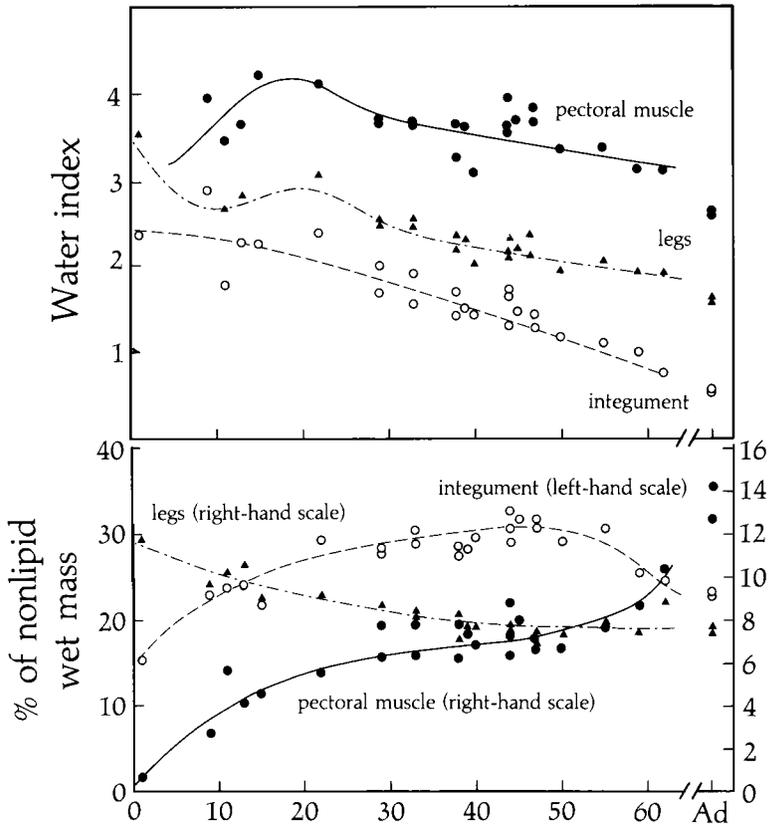


Fig. 7. Relationship between estimated age and the water index and proportion of nonlipid wet mass of the individual in pectoral muscles, legs, and integument. Fasted birds are omitted. Curves drawn by eye.

wings, increasing in rate after the third week and reaching only about two-thirds adult level by fledging.

*Organ development.*—Changes in water index and relative size of the legs, pectoral muscles, and integument are shown in Fig. 7. The water indices of the leg and integument decrease in a pattern consistent with precocial development. In both components, the water index is relatively low at hatching and decreases to adult levels by 60 days, suggesting more or less complete maturation before fledging (63–70 days).

Growth curves of the integument, pectoral muscles, and leg are shown in Fig. 8. Exponential rates of growth, which are equal to the slope of the relationship of the natural logarithm of mass to age, of all three components are rapid during the first 10 days but slow abruptly thereafter.

*Increase in lipid-free body weight.*—Increase in the masses of nonlipid wet and nonlipid dry components are shown in Fig. 9. Both curves were fitted by Gompertz equations, which are superimposed on the data. The fitted constants are  $A = 40$  g,  $t_i = 9$  days, and  $K = 0.080$  days<sup>-1</sup> for nonlipid wet mass and  $A = 13.5$  g,  $t_i = 14.5$  days, and  $K = 0.063$  days<sup>-1</sup> for nonlipid dry mass. Estimates of  $K$  for lipid-

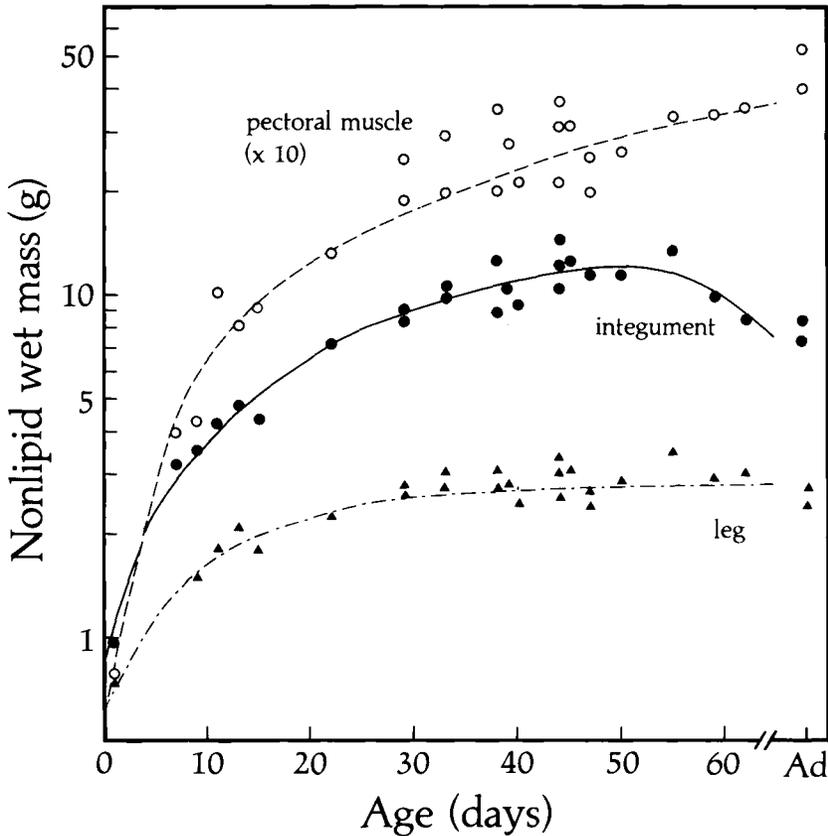


Fig. 8. Relationship between estimated age and the logarithm of nonlipid wet mass of the pectoral muscles, legs, and integument. Fasted birds are omitted. Curves drawn by eye.

free growth curves were similar to the value ( $K = 0.074$ ) fitted to Gross's weight data, at least compared to variation in values of  $K$  among species (Ricklefs 1973).

#### DISCUSSION

As in most species, changes in body proportion between hatching and adulthood include a decrease in the relative size of the head and increases in the relative sizes of wings and pectoral muscles. Compared to neonates of the European Starling (*Sturnus vulgaris*), Common Tern (*Sterna hirundo*), and Japanese Quail (*Coturnix coturnix*) (Ricklefs 1979a), the petrel neonate differed consistently only in having a slightly smaller head (16% vs. 19–20%). Its integument (15%) was of similar proportion to that of the semi-precocial tern (14%) and precocial quail (14%) and larger than that of the altricial starling (9%); its legs (12%) were of similar proportion to those of the starling (10%) but smaller than those of the tern (16%) and quail (18%). Adult petrels differ from the starling, tern, and quail in having proportionately more integument (23% vs. 12–20%), smaller pectoral muscles (13% vs. 16–20%), and less viscera (stomach, intestine, and liver: 10.5% vs. 13–17%).

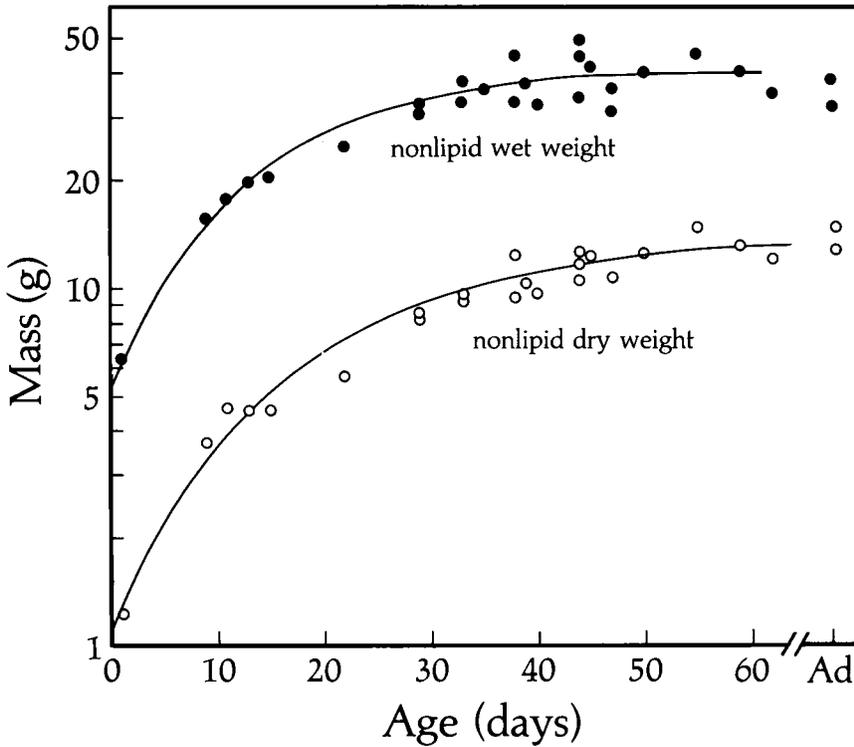


Fig. 9. Relationship between estimated age and the logarithms of total nonlipid wet mass and total nonlipid dry mass. Fasted birds are omitted. The lines are fitted Gompertz equations (see text).

Because the petrel neonate is large relative to the adult [about 16% of adult mass, compared to 7, 13, and 6% for the starling, tern, and quail (Ricklefs 1979a)], the overall postnatal growth increment of the petrel chick is relatively small (5.4 vs. 15, 8, and 20). As in most species, however, the integument, wings, and pectoral muscles (in sum, the flight apparatus) grow more rapidly than the body as a whole, while the head and some visceral organs grow more slowly. The mass of the pectoral muscles increases 59 fold between hatching and adulthood.

The water index of a tissue is inversely related to its functional maturity. Among neonates, this index calculated for the whole chick varies between 6 and 8 for altricial species (Ricklefs 1967b, 1975, 1979a, Brisbin 1969, Dunn 1975, Austin and Ricklefs 1977) and between about 3 and 4 in precocial species (Brisbin and Tally 1973, Clay et al. 1979, Ricklefs 1979a). The water index of the petrel neonate (4.1) places it with precocial species. Among the individual organs, only the water index of the stomach and intestines are within the range for altricial species, but in the adult petrel these organs have high indices as well.

As in most precocial species, the major feathers unsheath soon after they begin to grow, and the sheathed portion of the feather does not lengthen greatly. In the petrel, the feather sheaths are, at most, about 21% of the length of the adult primary and 15% of the length of the rectrix. Comparable values for starling, tern, and quail primaries are 35, 16 and 20%. In the petrel, the growth rates of feathers during the period of rapid linear increase were about 2.5 mm/day for the primary and 1.8 mm/

day for the rectrix. For primaries of the starling, tern, and quail, growth rates were 6.1, 5.1, and 2.5 mm/day. Expressed as a percentage of final length, these five values are 2.4 and 2.1 compared to 7.9, 2.5, and 4.6%/day.

Among species examined to date, the pectoral muscles of the petrel are extraordinary. Their water index during early postnatal development, before they have reached one-tenth of adult size, is approximately 3.5–4.0. At a comparable size, the water indices of pectoral muscles in the Japanese Quail and Common Tern are between 5 and 6 (Ricklefs 1979a). In the tern, the water index of the pectoral muscles does not fall to 4 until the last week before fledging. In the quail, the water index rapidly drops to about 4 during the first 2 weeks, just before the onset of flight (Ricklefs 1979a). If water index is a measure of tissue function, the development of the pectoral muscles in the petrel is similar to that in the quail, even though petrels do not attempt their first flight until 6 weeks later than quail chicks.

The uniqueness of the petrel's pectoral muscles can also be seen in the rate of increase in their relative size. In other species that, like the petrel, do not fly until fully grown, the pectoral muscles are relatively small until the last half of the period between hatching and fledging (Ricklefs 1979a). In the petrel, the pectoral muscles increase to 5% of total nonlipid wet mass of the chick by 10 days (Fig. 7) and have attained half of the adult size by 30 days of age (Fig. 8), fully a month before they are used in flight. Meanwhile, the relative size of the integument increases from 15% of nonlipid wet mass at hatching to about 30% during the latter half of the nestling period. Decrease in the relative proportion of integument to the adult level before fledging results from loss of water from maturing feathers. The relative size of the legs decreases steadily during the nestling period from 12% of the nonlipid wet mass of the neonate to 7.5% of the fledgling.

During the initial phase of rapid development, between days 1 and 10, the legs grow at an average exponential rate of about 10% per day (log of mass at end of interval minus log of mass at beginning, divided by length of interval). In the tern and quail, early growth of the leg averages about 6% per day, in the starling nearly 40% per day. In the last three species, exponential growth rate at a particular age is inversely related to the level of function achieved (Ricklefs 1979b). Both water index and growth rate indicate that the legs of the petrel develop precocially.

The exponential rate of growth of the pectoral muscles of the petrel averages about 24% per day during the first 10 days. In the tern and starling, which do not fly until fully grown, growth rates of the pectoral muscles are on the order of 20% per day or more throughout most of the development period. In the quail, the muscles grow at an average rate of about 19% per day during the first 3 weeks and then more slowly as their function develops (Ricklefs 1979a). In the petrel, between 10 and 40 days, the average growth rate of the pectoral muscles is 5% per day, a level that is consistent with well-developed function, yet the bird does not fly for another 3 or 4 weeks.

Our results indicate, first, that certain aspects of the development of Leach's Storm-Petrel chicks are similar to those of precocial species and, second, that the prolonged developmental period of the Leach's Storm-Petrel is consistent with its precocious mode of development. One need not invoke energy savings to explain slow growth. In addition, growth rate and water level point to the leg muscles and subsequently to the pectoral muscles as the tissues that constrain postnatal growth.

Our metabolic studies (Ricklefs et al. 1980) show that Leach's Storm-Petrel chicks are able to maintain their body temperatures in the nest burrow, where the ambient

temperature varies between 5 and 15°C, virtually from hatching. Chicks are rarely brooded beyond 5 days; small chicks have high metabolic rates and a strong thermogenic response to cold. In birds, thermogenesis is a function primarily of skeletal muscles (Calder and King 1974, West 1965). Neonates of most precocial species have large, well-developed leg muscles, which presumably provide heat as well as mobility. Heat production can be supplemented by the pectoral muscles as they grow and mature, depending upon the age at first flight (Aulie 1976).

In the petrel chick, the legs initially are small, and their proportion of body weight decreases with age. Nevertheless, at prevailing ambient temperatures, the specific metabolic rate of young Leach's Storm-Petrels ( $5-6 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ ) (Ricklefs et al. 1980) exceeds that of the larger neonates of the Common Tern ( $3-4 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) (Ricklefs and White MS) and Black-headed Gull (*Larus ridibundus*) ( $3-4 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) (Palokangas and Hissa 1971). At hatching, most of the petrel chick's metabolic heat must be generated by the legs. Within 10 days, however, the contribution of the pectoral muscles probably could equal that of the legs; of the leg component, less than half is skeletal muscle.

We propose the following explanation for slow growth in storm-petrels. First, petrel chicks are thermally independent of their parents after the first week. Second, because of their pelagic, surface-feeding habit, the adults have relatively small legs. The legs of the neonate also are small. Third, to generate the heat required for temperature regulation, the chick must rely on the early attainment of large size and maturation of its legs and pectoral muscles. The inverse relationship between growth rate and function dictates that the subsequent growth of these tissues must be greatly protracted and that age at first flight is delayed accordingly. Ricklefs (1979a, b) has argued that, among precocial species, the growth increment of the leg determines the length of the postnatal development period. In the petrel, that increment (a ratio of 3.5) is sufficiently small to permit more rapid growth of the body as a whole; indeed, the leg attains adult size within 30 days. For comparison, in the Japanese Quail the growth increment of the leg is a ratio of 17.7. It is possible, therefore, that in the petrel the large growth increment of the pectoral muscles (59) and their early maturation limit the pace of development during the latter part of the nestling period.

Hypotheses relating slow growth in petrels to food limitation and nutrient accumulation are explored more fully elsewhere (Ricklefs et al. 1980). The findings reported here are consistent with the inverse relationship between growth rate and precocity suggested for most species by Ricklefs (1973; 1979a,b).

#### ACKNOWLEDGMENTS

We are indebted to C. E. Huntington for advice, encouragement, logistical support, and permission to use unpublished data, to J. McEnroe for field assistance and unpublished data, and to D. Snyder for field assistance. I. L. Brisbin, M. Coulter, E. H. Dunn, and C. E. Huntington provided helpful comments on the manuscript. The study was supported by NSF Grants GB 31554X and GB 42661 to the senior author.

#### LITERATURE CITED

- AINLEY, D. G., S. MORRELL, & T. J. LEWIS. 1975. Patterns in the life histories of storm petrels on the Farallon Islands. *Living Bird* 13: 295-312.
- AINSLIE, J. A., & R. ATKINSON. 1937. On the breeding habits of Leach's Fork-tailed Petrel. *Brit. Birds* 30: 234-248.

- AULIE, A. 1976. The pectoral muscles and the development of thermoregulation in chicks of Willow Ptarmigan (*Lagopus lagopus*). *Comp. Biochem. Physiol.* 53A: 343-346.
- AUSTIN, G. T., & R. E. RICKLEFS. 1977. Growth and development of the Rufous-winged Sparrow (*Aimophila carpalis*). *Condor* 79: 37-50.
- BALDWIN, S. P., H. C. OBERHOLSER, & L. G. WORLEY. 1931. Measurements of birds. *Sci. Publ. Cleveland Mus. Nat. Hist.* 2: 1-165.
- BENT, A. C. 1922. Life histories of North American petrels and pelicans and their allies. *U.S. Natl. Mus., Bull.* 121.
- BRISBIN, I. L., JR. 1969. Bioenergetics of the breeding cycle of the Ring Dove. *Auk* 87: 54-74.
- , & L. J. TALLY. 1973. Age-specific changes in the major body components and caloric value of growing Japanese Quail. *Auk* 90: 624-635.
- CALDER, W. A., & J. R. KING. 1974. Thermal and caloric relations of birds. Pp. 259-413 in *Avian biology*, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- CLAY, D. L., I. L. BRISBIN, JR., & K. A. YOUNGSTROM. 1979. Age-specific changes in the major body components and caloric values of growing Wood Ducks. *Auk* 96: 296-305.
- DUNN, E. H. 1975. Growth, body components and energy content of nestling Double-crested Cormorants. *Condor* 77: 431-438.
- HARPER, P. C. 1976. Breeding biology of the fairy prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. *New Zealand J. Zool.* 3: 351-371.
- GROSS, W. A. O. 1935. The life history cycle of Leach's Petrel (*Oceanodroma leucorhoa*) on the outer sea islands of the Bay of Fundy. *Auk* 52: 382-399.
- LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.
- NICE, M. M. 1962. Development of behavior in precocial birds. *Trans. Linnean Soc. New York* 8: 1-211.
- PALMER, R. S. (Ed.). 1962. Handbook of North American birds, Vol. 1. New Haven, Yale Univ. Press.
- PALOKANGAS, R., & R. HISSA. 1971. Thermoregulation in young Black-headed Gull (*Larus ridibundus* L.). *Comp. Biochem. Physiol.* 38A: 743-750.
- RICKLEFS, R. E. 1967a. A graphical method of fitting equations to growth curves. *Ecology* 48: 978-983.
- . 1967b. Relative growth, body constituents and energy content of nestling Barn Swallows and Red-winged Blackbirds. *Auk* 84: 560-570.
- . 1968. Patterns of growth in birds. *Ibis* 110: 419-451.
- . 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115: 177-201.
- . 1975. Patterns of growth in birds. III. Growth and development of the Cactus Wren. *Condor* 77: 34-45.
- . 1979a. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. *Auk* 96: 10-30.
- . 1979b. Adaptation, constraint, and compromise in avian postnatal development. *Biol. Rev.* 54: 269-290.
- , & S. C. WHITE. 1975. A method for constructing growth curves from brief visits to seabird colonies. *Bird-Banding* 45: 135-140.
- , & ———. 1978. Growth rate of the Brown Noddy (*Anous stolidus*) on the Dry Tortugas, June 1972. *Bird-Banding* 49: 301-312.
- , ———, & J. CULLEN. 1980. Energetics of postnatal growth of Leach's Storm-Petrel. *Auk* 97: 566-575.
- WEST, G. C. 1965. Shivering and heat production in wild birds. *Physiol. Zool.* 38: 111-120.
- WILBUR, H. M. 1969. The breeding biology of Leach's Petrel, *Oceanodroma leucorhoa*. *Auk* 86: 433-442.