ENERGETICS OF POSTNATAL GROWTH
IN LEACH'S STORM-PETREL[1]

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ABSTRACT.—We measured the consumption of oxygen and the accumulation of energy in fat and tissues of nestling Leach's Storm-Petrels (Oceanodroma leucorhoa) on Kent Island, New Brunswick. Fat deposits of the chicks increased by an average of about 0.4 g·day^{-1} to a maximum of 30–35 g at 55–60 days. The rate of increase of nonlipid dry matter in tissues declined steadily from 0.25 g·day^{-1} during the first week to half that level by 40–50 days and to 0 by 60 days. Chicks could maintain their body temperatures above 35°C at an ambient temperature of 15°C from hatching, but temperature regulation was erratic during the first week. Mass-specific oxygen consumption at temperatures of 15–25°C averaged about 5 cc O_2·g^{-1}·h^{-1} during the first 5 days, dropping to less than 3 cc O_2·g^{-1}·h^{-1} by 20–30 days old. Adult petrels consumed an average of about 3.0 cc O_2·g^{-1}·h^{-1}. Oxygen consumption did not vary between day and night. We calculated an energy budget for petrel chicks based on the rate of accumulation of energy in fat and tissues and on the energy equivalent of oxygen consumption. According to our calculations, the energy requirement of the chick increases rapidly from 45–50 kJ·day^{-1} during the first 5 days to a plateau of 90–100 kJ·day^{-1} between 30 and 60 days. During the last two-thirds of the nestling period, the accumulation of tissue accounts for less than 5% of the energy requirement, whereas lipid accumulation is responsible for about 17% of the total. The remainder is divided between maintenance and temperature regulation. We did not obtain data during the week prior to fledging, when chicks metabolize most of the lipid they accumulate as nestlings. We suggest that variation in growth rate would have little effect on the total energy requirement of the chick and that the slow growth rate of petrel chicks is not an adaptation to reduce energy requirements. *Received 4 September 1979, accepted 6 March 1980.*

CHICKS of most procellariiform birds grow slowly and accumulate large quantities of lipid. Petrels, shearwaters, and their relatives forage far from nesting colonies for prey that, presumably, are sparce and unpredictably distributed. The single-egg clutch of all procellariiform birds suggests that their ability to deliver energy to the brood is severely limited, which has been verified experimentally by twinning studies (e.g. Huntington in Palmer 1962, Rice and Kenyon 1962, Harris 1966). Slow growth might be an adaptation to reduce the rate at which chicks require energy for development, thereby enabling parents to utilize more sparse or inaccessible food resources for breeding (e.g. Lack 1968). The lipid reserves of petrel chicks are thought to provide energy during intervals between feedings that commonly last from one to several days, depending upon the species, and longer when storms make foraging more difficult.

To evaluate the role of tissue growth and accumulation of lipid in the energy budgets of procellariiform chicks, we studied the growth and metabolism of nestling Leach's Storm-Petrels (Oceanodroma leucorhoa: Hydrobatidae) on Kent Island, New Brunswick, and supplemented our data with observations on Baccalieu Island,

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Newfoundland. Our objectives were to measure the rate of increase of lipid and other organic components during growth and the respiratory metabolism of chicks throughout the development period. From these data, we have constructed a preliminary energy budget for the storm-petrel chick.

METHODS

The breeding biology of Leach's Storm-Petrels in eastern North America has been described by Bent (1922), Gross (1935), Palmer (1962), and Wilbur (1969). Development of young is described in detail by Ricklefs et al. (in press).

This study was conducted primarily at the Bowdoin Scientific Station on Kent Island, New Brunswick, between 24 and 28 July and between 1 and 8 September 1972. Accumulation of lipid and nonlipid dry matter during growth was estimated from the composition of 24 chicks, collected between the ages of 1 and 62 days. Age criteria were based on the unpublished data of C. E. Huntington and J. McEnroe from Kent Island (see Ricklefs et al. in press). Ages of chicks less than 3 weeks old were estimated from mass (primarily) and wing length, while ages of older chicks were estimated solely by wing length. Measurements of chicks of known age indicated that most of our estimates were in the range of ±3 days of true values. Specimens were dried under a vacuum at 40–45°C, extracted in a 5:1 mixture of petroleum ether and chloroform, and ashed in a muffle furnace at 550°C (Ricklefs 1975, Ricklefs et al. 1980). We used the following conversion factors to calculate the accumulation of energy in biomass: lipid = 38 $kJ \cdot g^{-1}$ and nonlipid dry matter = 20 $kJ \cdot g^{-1}$ (Ricklefs 1974).

We measured temperatures with a Yellow Springs Instruments thermistor thermometer calibrated against a laboratory mercury thermometer in a water bath. To obtain body temperatures, we extended the thermistor down the esophagus into the proventriculus. We used an Ohaus triple-beam balance (scale to 0.1 g) to measure mass.

We measured oxygen consumption of chicks and several adults in a closed circuit apparatus consisting of a chamber for the bird, a small chamber fitted with a thermometer and oxygen-sensing probe, and tubes containing silica gel to remove water and potassium hydroxide to remove carbon dioxide. Air was circulated through the system with a diaphragm pump, and oxygen concentration was measured with a Beckman Fieldlab oxygen analyzer. We determined the volume of the system by filling it with water. The volume, 900 cc with a small chamber for the bird and 1,825 cc with a large chamber, was never less than 20 times the mass of the chick. In calculating the rate of oxygen consumption, the volume of air in the system was adjusted by subtracting the mass of the bird. Systematic biases produced by neglecting the density of the bird were less than 1%. Most measurements were made at ambient temperatures in an unheated building, but we used an incandescent light in a box to obtain higher ambient temperatures for some trials. We did not determine whether light itself influenced metabolism independently of raising ambient temperature. Birds were left in the metabolism chamber until the oxygen concentration had been reduced from 21% to 18 or 19%.

We supplemented our data on oxygen consumption by small chicks with measurements obtained on Baccalieu Island, Newfoundland, during late July 1978. There, oxygen consumption was measured by volume change in a small chamber having cloth bags of soda lime to absorb carbon dioxide and silica gel to absorb water vapor. Volume of oxygen consumed was measured by the rate at which a drop of water was pulled through a capillary tube having a volume of 0.0166 $cc \cdot cm^{-1}$. Measurements were continued during each trial until a repeatable value was obtained.

Values reported for oxygen consumption are volumes of oxygen adjusted to standard temperature (0°C) and sea level pressure (760 mm Hg). The energy equivalent of oxygen is 20.1 $kJ \cdot 1^{-1}O_2$.

We determined rates of defecation in eight trials of 12–15 h duration. Chicks whose estimated ages were 25–58 days were taken from burrows at either 0600 ($n = 4$) or 1800 ($n = 4$) and kept in small plastic boxes with a raised floor of ½-inch mesh hardware cloth over an aluminum foil-lined bottom. At the end of each trial, the droppings were dried, scraped from the foil, and weighed.

RESULTS

Mass.—In Fig. 1A, masses of 24 chicks collected in this study (solid symbols) are graphed as a function of estimated age. Plotted on the same graph are the masses of chicks whose metabolism we measured (open symbols). The upper line drawn on the graph in Fig. 1A follows the trend of the daily averages of measurements of 19
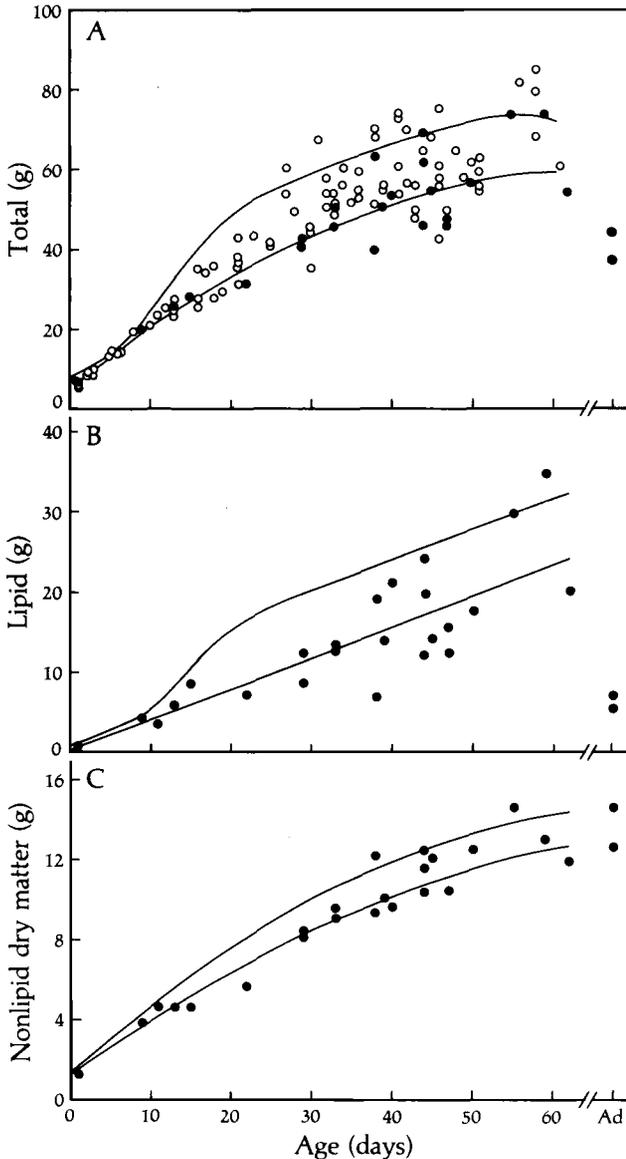
Fig. 1. Masses of chicks (A) and their contents of lipid (B) and nonlipid dry matter (C) as a function of estimated age. Solid symbols represent chicks that were collected for biochemical analysis; open symbols represent birds used in metabolism trials. Lower lines express the trend among chicks collected for analysis in 1972. Upper line in A is the average of chicks weighed by C. E. Huntington in 1962. Upper lines in B and C were drawn in the same relationship to values for collected chicks as the upper line in A.

chicks weighed by C. E. Huntington on Kent Island in 1962 (see Ricklefs et al. in press). The lower line was drawn by eye to represent the trend among specimens collected in 1972.

The accumulation of lipid and nonlipid dry matter (mostly protein and ash) by chicks is shown in Figs. 1B and 1C. Lipid appears to increase at an average rate
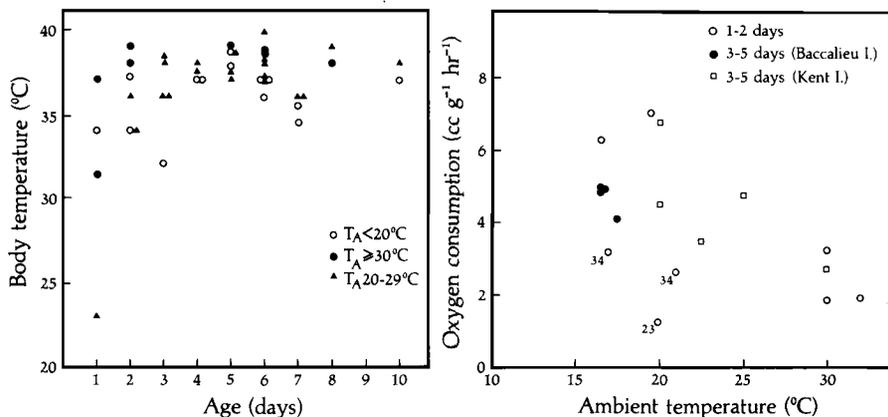
Fig. 2. Left: Body temperatures of petrel chicks 1–10 days old after exposure to various ambient temperatures (T_A) during measurements of oxygen consumption. Right: Relationship of the rate of oxygen consumption to ambient temperature among chicks less than 6 days old. Body temperatures of three hypothermic chicks are indicated on the graph.

of about 0.4 g·day^{-1} to at least 60 days. Two of the oldest chicks (estimated ages 55 and 59 days) had 30 and 35 g of lipid. Like other procellariiforms, petrel chicks lose mass rapidly during the last week of the nest period (Huntington, unpubl. data) when, presumably, most of the accumulated lipid is metabolized. By the end of our study, however, none of the chicks had apparently entered this prefledging phase.

Nonlipid dry matter was accumulated at a rate that decreased from about 0.25 g·day^{-1} during the first week to half that level or less by 40–50 days (Fig. 1C). By 60 days, chicks had accumulated nonlipid dry material equivalent in mass to that of the adult.

In Figs. 1B and 1C, the upper and lower curves were drawn in approximately the same relationship to the solid symbols as the corresponding curves in Fig. 1A. Hence, the upper curves suggest what the average trend for lipid and nonlipid dry matter might have been for the chicks weighed in 1962; the lower curves indicate conservative estimates of the trends in 1972.

To estimate the degree of variation among chicks and confidence limits for average values, we calculated the standard deviations and standard errors of the average rates of accumulation of lipid and nonlipid dry material for chicks whose estimated ages were 30–62 days. Rates of accumulation were calculated by dividing the increment in mass since hatching by estimated age. Initial masses of lipid and nonlipid dry matter were 0.7 and 1.2 g $(n = 1)$. Rates of accumulation averaged 0.221 g·day^{-1} ± 0.032 SD (14% of average) and 0.008 SE $(n = 17)$ for nonlipid dry matter and 0.373 g·day^{-1} ± 0.122 SD (33%) and 0.030 SE $(n = 17)$ for lipid. The correlation coefficient relating rates of accumulation of lipid and lean dry matter was $r = 0.44$ $(0.10 > P > 0.05)$. Hence, the two rates may be treated as being independent.

Temperature.—Temperatures in the burrows of Leach's Storm-Petrels on Kent Island vary mostly within the range 10–15°C during the chick stage. D. Ainley (unpubl. data) kept a continuous record of temperatures in one unoccupied burrow and one occupied burrow between 1 July and 10 August 1967 on Kent Island. Minimum daily temperatures varied between 4.4 and 6.7°C in the unoccupied burrow, 10.0 and 12.2°C in the occupied burrow, and 6.1 and 8.9°C at ground level

near the burrows. Maximum daily temperatures varied between 5.0 and 7.8°C, 10.1 and 15.6°C, and 9.4 and 19.4°C, respectively. Relative humidity in the burrows was 92–100%. Temperatures in one burrow occupied by an adult and egg during one 12-day period in July 1978 varied between 8 and 9°C (H. Rahn, unpubl. data). On Baccalieu Island, temperatures in five burrows occupied by small chicks on a sunny slope at 1530 on 23 July 1978 (shade temperature 19°C) varied between 13.0 and 15.8°C.

Leach's Storm-Petrels are capable of thermogenesis from hatching, although their body temperatures fluctuate during the first 5 days. Petrel chicks apparently are brooded during the first 3–5 days after hatching (Huntington, in Palmer 1962). C. E. Huntington and P. Walls (unpubl. data) measured body temperatures of chicks in burrows in 1962 on Kent Island. Most of their measurements of the temperatures of birds less than 10 days old were recorded from one chick and were as follows: day 1, 28.5°C; day 3, 34.5°C; day 4, 35.8°C; day 5, 27.0°C; day 6, 36.0 and 37.3°C; day 7, 23.6 and 37°C; day 8, 30.4°C; and day 9, 36.5 and 37.0°C. In larger samples of older chicks, average body temperature increased from about 37°C between day 10 and 15 to 37.5°C at day 15 and between 38.0 and 38.5°C at day 30 and thereafter.

Between 25 and 28 July 1972, we recorded the following temperatures of small petrel chicks of known age immediately upon removing them from their burrows: day 1, 35.0°C; day 2, 38.2°C; day 3, 38.1 and 24.5°C; day 4, 38.9°C; day 5, 38.0°C. In a sample of 10 chicks whose estimated ages were 6–17 days, the average temperature was 38.4°C ± 0.2°C SE (range, 37.4–39.8°C). On 1 September 1972, between 0830 and 1130, in a sample of 28 chicks whose estimated ages were 5–50 days, body temperature varied between 38 and 39.9°C, with an average of 39.0°C ± 0.1°C SE. In addition, we recorded temperatures of 22°C from a 30-day-old chick weighing 48 g and 34.5°C from a 40-day-old chick weighing 51 g. These measurements indicate that homeothermy is well-established by 5 days of age and that body temperatures are generally maintained above 37°C but do not exceed 40°C. The two older hypothermic chicks discovered in burrows were not unusually light (cf. Fig. 1A).

Temperatures of 1- to 10-day-old chicks at the end of metabolism trials are shown in Fig. 2A. Most of these chicks had been kept in small containers without insulation at 15°C for a half hour or more before the trial. They exhibited a strong capacity for generating heat from hatching but erratic control of body temperature during the first week. Among chicks older than 10 days, only one had a temperature below 38°C after the metabolism trial. It was a 22-day-old, 32.8-g chick; its temperature was 29.5°C and its mass-specific metabolism was very low (1.17 cc $O_2 \cdot g^{-1} \cdot h^{-1}$).

Metabolism.—We measured oxygen consumption under conditions as close to natural as possible. None of the chicks was fasted more than a day, which is the shortest feeding interval for this species. We were not, however, able to obtain ambient temperatures below 16°C, and the relative humidity and degree of insulation and convection were not measured and could have differed considerably from those in nest burrows. Leach's Storm-Petrel chicks are extremely docile. They were not active in the chambers, nor is it likely that they are active in their burrows.

Among chicks 1–5 days old, rate of oxygen consumption increased with decreasing ambient temperature, from about 2.5 cc $O_2 \cdot g^{-1} \cdot h^{-1}$ at 30°C to between 5 and 8 cc $O_2 \cdot g^{-1} \cdot h^{-1}$ at 15–20°C (Fig. 2B). At the lower ambient temperatures, we recorded values below 3.5 cc $O_2 \cdot g^{-1} \cdot h^{-1}$ from 1- and 2-day-old birds with body temperatures

TABLE 1. Oxygen consumption of nestlings at ambient temperatures of 15–25°C.

				Estimated age (days)				
	1–5	6–10	11–20	21–30	31–40	41–50	>50	Adult
Total[a]								
n	10	9	23	25	37	32	14	14
x	54.3	74.0	94.6	126.6	147.6	164.2	161.8	126.2
SD	17.5	17.7	24.5	33.0	30.8	42.0	45.7	26.6
SE	5.5	5.9	5.1	6.6	5.1	7.4	12.2	7.1
Mass-specific[b]								
n	10	9	23	25	37	32	14	14
x	5.1	4.0	3.6	2.9	2.6	2.8	2.4	2.9[c]
SD	1.2	0.8	1.0	0.9	0.5	0.8	0.5	0.7
SE	0.4	0.3	.02	0.2	0.1	0.1	0.1	0.2

[a] Units are cc $O_2 \cdot h^{-1}$.
[b] Units are cc $O_2 \cdot g^{-1} \cdot h^{-1}$.
[c] Six values obtained from 3 adults on Baccalieu Island, at ambient temperature of 16–19°C, averaged 2.8 ± 0.1 SE cc $O_2 \cdot g^{-1} \cdot h^{-1}$. These determinations were based upon pressure changes in a closed system fitted with a water manometer.

of 23, 34, and 34°C. A linear regression fitted to the data in Fig. 2B, excluding 3 points representing chicks with low body temperatures, had a slope of -0.209 ± 0.051 SE [$F(1,12) = 16.6; P < 0.005$]. The predicted intercept on the x (temperature) axis was 43°C. The regression suggests that young petrel chicks have a thermal conductance with a metabolic equivalent on the order of 0.2 cc $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$. According to the empirically determined relationship of Lasiewski et al. (1967), the thermal conductance of adults of a species having a mass of 10 g is about 0.26 cc $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$. Hence, the insulation of the petrel neonate is similar to that of adult birds of the same size.

Rates of consumption of oxygen by petrel chicks at ambient temperatures between 15 and 25°C are compared by age class in Table 1. Measurements of oxygen consumption were distributed fairly evenly throughout the day and night. No diurnal rhythm in rate of oxygen consumption was noticed except for the fact that values below 2 cc $O_2 \cdot g^{-1} \cdot h^{-1}$ all occurred between 1200 and 1800 (estimated ages, > 10 days; ambient temperatures, $< 26°C$).

Within an age group, oxygen consumption was not strongly related to mass. Among chicks 30–39 days of age, whose masses ranged from 35 to 70 g ($x = 55.0$ g ± 7.5 SD), oxygen consumption was positively related to mass [$F(1,38) = 4.2$, $P < 0.05$]. But the slope of the relationship, $b = 1.25 \pm 0.61$ cc $O_2 \cdot g^{-1} \cdot h^{-1}$, was considerably less than the mass-specific rate of oxygen consumption for that age class (2.6 cc $O_2 \cdot g^{-1} \cdot h^{-1}$, Table 1), and only 10% of the variation in rate of oxygen consumption could be attributed to variation in mass. Among chicks 40–49 days of age, oxygen consumption was not significantly related to mass [$F(1,29) = 0.33, P > 0.50$].

Most of the chicks that we collected had their rate of oxygen consumption measured shortly before they were sacrificed. We were therefore able to relate oxygen consumption to quantities of lipid and nonlipid wet components. The following analysis is based on 19 chicks, whose estimated ages were 25–61 days and whose masses varied between 37 and 79 g. Amounts of lipid varied between 7 and 35 g, and amounts of nonlipid wet components varied between 24 and 44 g; the two were significantly correlated ($r = 0.66$, $P < 0.01$). Rate of oxygen consumption was weakly related to lipid content when the effect of variation in nonlipid dry matter

TABLE 2. Calculations of the energy budget of Leach's Storm-Petrel chicks.[a]

Age interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
0–5	54.3	0.40	0.28	15.2	5.6	20.8	26.2	27.7	19.3	47.0
5–10	74.0	0.40	0.24	15.2	4.8	20.0	35.7	26.7	29.0	55.7
10–20	94.6	0.40	0.25	15.2	5.0	20.2	45.6	26.9	38.9	65.8
20–30	126.6	0.40	0.21	15.2	4.2	19.4	61.1	25.8	54.7	80.5
30–40	147.6	0.40	0.17	15.2	3.4	18.6	71.2	24.7	65.1	89.8
40–50	164.2	0.40	0.13	15.2	2.6	17.8	79.2	23.7	73.3	97.0
50–60	161.8	0.40	0.10	15.2	2.0	17.2	78.1	22.9	72.4	95.3

[a] Explanation of columns:
(1) Oxygen consumption (cc $O_2 \cdot g^{-1} \cdot h^{-1}$) from Table 1.
(2) Rate of accumulation of lipid (g·day^{-1}); the slope of the lower curve in Fig. 1B.
(3) Rate of accumulation of nonlipid dry matter (g·day^{-1}); the slope of the lower curve in Fig. 1C.
(4) Energy equivalent of lipid accumulation (kJ·day^{-1}) = (2) × 38 kJ·g^{-1} lipid.
(5) Energy equivalent of accumulation of nonlipid dry matter (kJ·day^{-1}) = (3) × 20 kJ·g^{-1}.
(6) Energy equivalent of tissue accumulation (kJ·day^{-1}) = (4) + (5).
(7) Energy equivalent of oxygen consumption (kJ·day^{-1}) = (1) × 24 h·day^{-1} × 20.1 kJ·l^{-1} O_2 ÷ 1,000 ml·l^{-1}.
(8) Total energy requirement for growth (kJ·day^{-1}), assuming production efficiency of 75% = (6) × 1.33.
(9) Total energy expenditure for maintenance (kJ·day^{-1}) = (7) − 0.33 × (6).
(10) Total energy expenditure for growth and maintenance (kJ·day^{-1}) = (8) + (9).

was accounted for [$F(1,17) = 3.4$, $0.10 > P > 0.05$], but not vice versa [$F(1,17) = 0.005$, $P > 0.50$]. The simple regression of rate of oxygen consumption upon mass of fat had a slope of 2.8 cc $O_2 \cdot g^{-1} \cdot h^{-1}$ ± 1.1 SE [$F(1,17) = 6.4$, $P < 0.025$], which is similar to the mass specific rate of oxygen consumption. Within age classes of 10 day's breadth, rate of oxygen consumption was not related to mass (see above). Therefore, the significant positive relationship between rate of oxygen consumption and fat depended upon the wider range of ages used in the analysis.

Rate of defecation.—Eight chicks whose estimated ages were 25–58 days had defecation rates of 1.8 ± 0.9 SD mg dry mass·g^{-1}·day (range, 0.7–3.2) during 12–15-h trials.

DISCUSSION

With respect to temperature regulation, Leach's Storm-Petrel chicks develop precocially. Their ability to produce heat metabolically is consistent with slow growth and low water content of the legs and pectoral muscles (see Ricklefs et al. in press). The metabolic intensity of the chicks during the first five days after hatching averaged about 5 cc $O_2 \cdot g^{-1} \cdot h^{-1}$, which is nearly double the basal metabolic rate of adult birds of similar size (Ascoff and Pohl 1970).

We constructed an energy budget for Leach's Storm-Petrel chicks (Table 2) calculated in the following manner. Rates of accumulation of lipid and nonlipid dry material were obtained from Figs. 1B and 1C and converted to energy equivalents (accumulated energy). We assumed that the cost of biosynthesis is about one-third the accumulated energy (Ricklefs 1974), and we therefore multiplied the accumulated energy by 1.33 to obtain the growth energy. Maintenance energy is the metabolic equivalent of oxygen consumption minus the cost of biosynthesis. Total energy is the sum of growth and maintenance. The energy requirement of activity was assumed to be negligible. Energy excreted in the feces probably amounts to no more than 0.05 kJ·g^{-1}·day^{-1}, and we have ignored it in our calculations.

The energy budget of the petrel chicks is shown in Fig. 3. Total energy requirement increases gradually to its maximum, approximately 90–100 kJ·day^{-1} by day
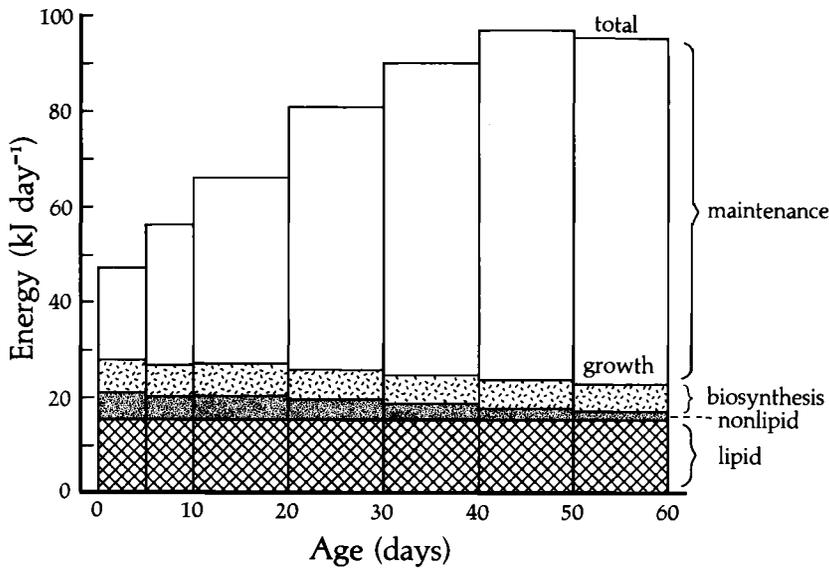
Fig. 3.   Daily energy budgets of petrel chicks at various ages estimated from rates of accumulation of lipid and nonlipid matter and consumption of oxygen (see text).

30. The growth energy requirement decreases from about 60% of the total shortly after hatching to 50% by 5–10 days, 33% by 20–30 days and 25% of the total before the end of the nestling period. Of the growth requirement, at least 75% results from the accumulation of lipid at all stages of development, excluding the final period of weight loss before fledging.

To estimate the degree of variation and confidence intervals about average values in the estimated energy budgets, we added the variances in the components used to estimate them, assuming independence. Any positive correlations between component values would tend to increase the estimated variance of the total, but we found little relationship among lipid levels, nonlipid dry matter, and metabolism. We give these calculations here for the age interval 30–40 days. Because the energy accumulated in nonlipid matter is small, its variation is a small fraction of the total (0.6 kJ SD and 0.2 kJ SE). That for lipid is much greater (5.0 kJ SD and 1.2 kJ SE). Adding the variances (squares of these values) and multiplying by 1.33 to account for the cost of biosynthesis, the variability in the growth energy requirement is ±5.8 kJ SD and 1.4 kJ SE. Variation in rate of oxygen consumption at 31–40 days was equivalent to ±11.5 kJ SD and 1.9 kJ SE. Added to the growth energy requirement, variation in the total comes to ±12.5 kJ SD (14% of total) and 2.3 kJ SE (3%). Therefore, 95% confidence limits for the average energy requirement of the chick are approximately ±6% of the estimated value.

The resting metabolic rate of adults (126.2 ± 7.1 SE cc $O_2 \cdot h^{-1}$) is equivalent to about 61 $kJ \cdot day^{-1}$, which is about twice the basal metabolic rate (BMR) predicted by Aschoff and Pohl's (1970) equation (31.6 $kJ \cdot day^{-1}$ for a mass of 45 g). If each parent contributed equally to feeding the chick, energy required by the chick would almost double the level of the resting metabolic energy requirement for each adult. Added to this would be the cost of travelling between feeding and nesting areas.

The peak energy requirement of Leach's Storm-Petrel chicks (90–100 kJ·day^{-1}) is equivalent to about 300% adult BMR, or 150% BMR per parent. If adults spent an average of 4 h per day flying between the feeding area and the nest (a 200-mile round trip every 2 days at 25 mi·h^{-1}) at a cost of 700% BMR (Utter and LeFebvre 1970), another 100% BMR would be added to the daily energy expenditure of each adult, bringing the total for reproduction to 250% BMR. Although this value is quite speculative, it lies within the range of energy requirements for reproduction of a temperate-zone passerine bird cooperating with its mate to rear four offspring (Ricklefs 1974). It is therefore conceivable that the rate of food gathering by petrels is comparable to species in other orders rearing larger broods. If this were true, the one-egg clutch of the petrel would reflect the high energy demands of the young and the unproductive time and energy expended to fly between nesting site and feeding area, rather than the availability of the food supply itself.

Lack (1968) and others have suggested that the slow growth of procellariiform birds is an adaptation to reduce the energy requirement of the young. The energy budget in Fig. 3 does not support this view. After the maximum energy requirement of the young has been achieved, at about 30 days, accumulation of nonlipid dry matter (growth) amounts to less than 5% of the total energy expended. Therefore, rate of accumulation of tissue (excluding fat) could be doubled without adding more than 5% to the total food requirement. We have argued elsewhere (Ricklefs et al. in press) that the slow growth of the Leach's Storm-Petrel follows directly from its precocial development. In general, postnatal growth rates of procellariiforms are similar to those of precocial galliforms having the same adult mass (Ricklefs 1973).

Lipid reserves are thought to supply energy to the chick during the intervals between feeds and to provide insurance against long absences resulting from storms or poor feeding conditions. Lipid is accumulated at a fairly steady rate throughout most of the nestling period, with reserves perhaps doubling between the time the chick reaches its maximum energy requirement, at 30 days, and 60 days of age (Fig. 1B). With an energy requirement for maintenance of 90–100 kJ·day^{-1}, modest reserves of 15 g of lipid would supply the chick's needs for up to a week.

Although fat reserves undoubtedly act as a day-to-day energy supply and as long-term insurance, their primary function is not clear. In 1972 on Kent Island, when petrel chicks were probably somewhat undernourished, none of the birds older than 20 days had less than 7 g of lipid. Furthermore, rather than becoming adjusted to the metabolic requirements of the chick, the level of lipid accumulated continues to increase after the chick's energy expenditure has leveled off. This suggests that it is somehow important to accumulate energy throughout the development period. Because petrel chicks leave the nest when they are only slightly heavier than adults (Huntington, unpubl. data), most of their fat is metabolized during the week or so before fledging. At this time, adults make fewer feeding visits to the nest; indeed, shearwaters (*Puffinus*) abandon their young completely. Because there is no post-fledging parental care, the length of the feeding period can be shortened by an amount proportional to the lipid stored, provided that at the end of the nest period the chick does not require nutrients other than energy in large quantity. Petrel nestlings accumulate adult levels of nonlipid dry matter by 50–55 days of age (Fig. 1C), which is 1–2 weeks before fledging. It is difficult to identify an advantage to cutting short the period of parental feeding, although it may serve to reduce reproductive effort or risk or allow adults to begin postnesting dispersal earlier than they would otherwise.

Lipid deposition may be a direct consequence of the chick's diet, or it may serve to increase the energetic efficiency of development. The storm-petrels feed mainly upon planktonic crustacea having high lipid contents. Ashmole (1971) has suggested that the adults further concentrate the lipids in their stomachs by selectively assimilating and metabolizing nitrogenous components of the diet and excreting most of the water. By retaining lipid in the stomach to deliver to the chick, the adult can extend its foraging trip and increase the efficiency of transporting energy back to the nest, provided the chick can utilize the excess energy. By accumulating lipid during most of the growth period, the petrel chick might "allow" its parents to increase their foraging efficiency greatly, thereby providing for the chick under correspondingly poorer feeding conditions. Lipid storage increases by about one-fifth the energy delivered to older chicks per unit time and per foraging trip made by the parent. The parents could possibly realize the benefit of this energy storage at the end of the chick's growth period when the lipid is metabolized and their feeding rates are correspondingly reduced.

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