

CHICK ENERGY REQUIREMENTS AND ADULT ENERGY EXPENDITURES OF DOVEKIES (*ALLE ALLE*)

MAREK KONARZEWSKI,^{1,3} JAN R. E. TAYLOR,^{1,4} AND
GEIR W. GABRIELSEN^{2,5}

¹*Institute of Biology, University of Warsaw, Branch in Bialystok, Swierkowa 20 B, 15-950 Bialystok, P.O. Box 109, Poland; and*

²*The Norwegian Polar Research Institute, P.O. Box 158, N-1330 Oslo Lufthavn, Norway*

ABSTRACT.—We constructed an energy budget for Dovekie (*Alle alle*) chicks in West Spitsbergen by measuring energy metabolism, rate of accumulation of energy in growing tissues, and body water turnover rate, the last serving as the basis for energy-consumption calculations. The energy budget of a "typical chick" was calculated for chicks measured in 1986 and 1987. Mass-specific resting metabolic rate in Dovekie chicks peaked at days 7 to 10 and then declined considerably. Thermal conductance decreased by 60% between hatching and fledging. Energy deposition in growing tissues, resting metabolic rate, and energy consumption reached maximum values midway through the fledging period. Chicks examined in 1984 had 11% lower growth rate than 1986 and 1987 chicks, and their energy deposited in tissues between hatching and the age of peak body mass before fledging was 17% lower. Energy requirements of Dovekie chicks were much higher than those of other seabird chicks of similar body mass. We attribute this to the arctic nesting of Dovekies. We compared energy demands of Dovekie chicks with those of adults reported in another study. Despite high chick energy demands, energy delivered to the chick by one parent was only 15% of the total energy gathered by the parent (to meet both its own and the chick's needs). We suggest that this reflects a high cost of foraging in adult Dovekies. Additionally, high energy demands of chicks may contribute to the high energy expenditures of adults. This may be a major contribution to the restriction of a Dovekie brood to one chick and to the low chick body mass at fledging. Received 6 January 1992, accepted 27 May 1992.

THE ABILITY of parents to provide food for offspring is generally considered a major factor shaping reproductive strategies of birds with nidicolous young. Parents should raise the greatest possible number of young permitted by food availability (Lack 1968) and optimized with respect to the trade-off between investment in a given brood and probability for future reproductive success (Williams 1966, Charnov and Krebs 1974). Brood-size reduction is the primary means of matching reproductive effort to declines in parental foraging capacity. Depression of chick growth rate is a means of fine tuning the adjustment. The latter is especially

important in birds that lay small clutches, where the integer steps of adjusting clutch size become too crude (Ricklefs 1968). The adaptive value of growth rate adjustment is based on the assumption that change in growth rate results in substantial change in chick energy requirements, but this assumption has not been consistently supported (for a recent discussion see Klaassen et al. 1992).

Seabirds have much lower reproductive rates than most terrestrial birds (Lack 1968). In many seabird species, adults lay one-egg clutches, forage at long distances from their breeding colonies, and feed their chicks infrequently. Presumably, the severely limited ability of adult birds to deliver food requires that reproductive effort be adjusted to a minimum anticipated level, resulting in slow chick growth in most seabird species (Ricklefs 1983).

Among seabirds, alcids (family Alcidae) offer a good opportunity for comparative studies of growth patterns and factors leading to clutch reduction. Alcids exhibit three patterns of post-hatching development: precocial, semiprecocial, and intermediate. Chicks of intermediate

³ Current address: Department of Physiology, University of California Medical School, Los Angeles, California 90024, USA.

⁴ Current address: Alaska Cooperative Fish and Wildlife Research Unit, 209 Irving Building, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA.

⁵ Current address: Norwegian Institute for Nature Research, University of Tromsø, c/o Tromsø Museum, N-9000 Tromsø, Norway.

species go to sea when flightless and weighing only about one-quarter of adult mass. Semiprecocial alcid stay in the nest much longer, exhibiting a wide variety of growth patterns (Searly 1973).

In an attempt to shed light on why Dovekies (*Alle alle*) lay single-egg clutches and on the selective forces shaping their growth pattern, we studied energy requirements of Dovekie chicks. The Dovekie is a small (160-g) planktivorous alcid that breeds only in the Arctic and raises a single semiprecocial chick (Birkhead and Harris 1985). The growth rate of Dovekie chicks is not as low as in many seabird species, but at fledging they attain only 65 to 70% of adult body mass (Stempniewicz 1980, Konarzewski and Taylor 1989). The average nestling period is 27 days and they attain peak nestling body mass in three-fourths of that time. Then there is a slight recession in body mass prior to fledging, but chicks continue to grow feathers and accumulate macroelements in their bodies (Stempniewicz 1980, Taylor and Konarzewski 1992).

We studied energy accumulation and metabolism, and constructed energy budgets for Dovekie chicks. We also compared energy requirements of chicks with those of their parents (reported in Gabrielsen et al. 1991). We calculated the energy delivered to the chick as a ratio of total energy gathered by the parent, and compared it with the same ratio in other alcid species, as well as with diving-petrels (alcids' ecological counterparts in the Southern Hemisphere). Metabolic rates of adult Dovekies feeding chicks are extremely high (Gabrielsen et al. 1991), and we attempted to determine to what extent the energy requirements of chicks contribute to high energy-expenditure rates of adults.

MATERIALS AND METHODS

All chicks used in this study were from the Dovekie colony on the southern slopes of the Arie Mount (Ariekammen), Hornsund Fjord, West Spitsbergen (77°00'N, 15°22'E). Marked nests were inspected daily at the time of hatching and the ages of chicks, thus, were known to within one day.

Chicks used for the determination of energy content in tissues and, hence, energy accumulation with growth were collected in 1984, 1986 and 1987. The same chicks also were used for analyses of gross body composition (water, petroleum ether-extractable lipids, lean dry mass) reported in Taylor and Konar-

zewski (1989). All details of collection methods and carcass analysis are given in that paper.

The dry homogenates from 64 chicks collected in 1984 and from 19 of 37 chicks collected in 1986 were combusted in a Berthelot-type adiabatic bomb calorimeter. Two or three 1-g aliquots from each chick were used. Birds represented all developmental stages up to the fledging age of 27 days. The regression line of energy density on fat content (%) in the dry chick carcasses was calculated and used for prediction of energy densities of all 1986 and 1987 chicks (these chicks were used to calculate energy budget of a "typical chick"; see Results). Energy density of fresh tissue was obtained by correcting the energy density of dry material for natural water content. To avoid inconsistency due to different methods of determination of energy content of 1984 and 1986-1987 chicks, the statistical interyear comparison of chick energy contents was performed on the values derived from the body composition, assuming 1 g fat is equivalent to 38 kJ, and 1 g of dry nonlipid matter is equal to 20 kJ. Such energy contents were on average 1% lower than those from direct determination.

The measurements of metabolic rate of the chicks were made in 1987 in the Polish Polar Station at Hornsund, 1 km south of the bird colony. Oxygen consumption and carbon-dioxide production of chicks were measured with a flow respirometer "Spirolyt" (Junkalor) with a paramagnetic analyzer for O₂ and diaferrometric for CO₂. Chicks were tested in 0.3- to 1.4-L chambers, depending on chick age and size. The rate of air flow through the chamber was set between 10 and 30 L/h, which produced an increase in CO₂ content in the expired air not exceeding 1.2% that of ambient air. The air leaving the chamber passed through silica gel to remove water before entering the analyzers. The chicks were placed in the chambers within 30 min of removal from the nest. Measurements on one- and three-day-old, largely poikilothermic chicks were taken at air temperatures in the chamber of 25° to 30°C, and 25°, respectively. Air temperature measured in the chamber was stabilized within ±0.5° by submersion of the chamber in a water bath. The chambers with older (homeothermic) chicks were placed outdoors; hence these measurements were performed in 5° to 10°, which approximates well the range of air temperatures in Dovekie nest crevices during chick rearing (Konarzewski and Taylor 1989). Trials lasted 1.5 to 2.5 h with gas exchange recorded over the last 20 to 30 min. Trials were prolonged when birds were excessively active, and some measurements were excluded from calculations due to chicks' restlessness. Body temperature of the chicks was measured immediately after each trial with a thermistor probe (±0.1°C) inserted 3 to 4 cm into the cloaca. After the experiments, all birds were returned to their nests, where they were invariably accepted by their parents. Body temperatures of other chicks, one to five days old, were also measured in the colony immediately

after removal from the nest. All measurements were taken between 0900 and 2000 local time.

All gaseous values were converted to standard conditions (STP). When converting gasometric data into energy values, the caloric equivalent of oxygen volume was determined independently for each measurement according to the observed respiratory quotient. Thermal conductance of chicks ($\text{ml O}_2/[\text{g h } ^\circ\text{C}]$) was calculated as:

$$\text{VO}_2/[(T_b - T_a)M], \quad (1)$$

where VO_2 is oxygen consumption ($\text{ml O}_2/\text{h}$), T_b is body temperature ($^\circ\text{C}$), T_a is ambient temperature ($^\circ\text{C}$), and M is body mass (g).

The energy consumed by chicks was calculated from water-influx rates measured in the chicks in the colony in 1986 using the tritiated-water method (Lifson and McClintock 1966, Nagy and Costa 1980), and known water and energy content of food. In the field, chicks were injected with 0.4 ml tritiated water (containing 0.32 mCi tritium) into the pectoral muscle using a laboratory-calibrated syringe. We allowed 1 h for the tritiated water and body water to equilibrate, after which each chick was returned to its nest, it was weighed to the nearest 0.1 g, and a blood sample (20–30 μl) was taken from the vein in the foot. Second and third blood samples were taken from each chick after 12 and 24 h; thus, each chick gave two 12-h measurements of water flux rates. Near-fledging chicks (25 to 26 days) were bled only once (after 24 h). Two background blood samples were taken from uninjected chicks. The blood samples were stored in flame-sealed, heparinized microhematocrit tubes, and were vacuum-distilled to obtain pure water. The water was assayed for tritium activity by liquid-scintillation spectrometry. Water efflux and influx were calculated using equations 4 and 6, respectively, of Nagy and Costa (1980). The volume of water (TBW, ml) in the body of each bird at each sampling time was estimated from regression equations calculated from raw data of Taylor and Konarzewski (1989), relating TBW to live wet mass (M , g) in chicks collected in 1986 and 1987. These data were obtained by drying chicks to constant mass. For young chicks (4 to 13 days of age),

$$\text{TBW} = 3.12 + 0.6485 M \quad (2)$$

($\text{SE} = 0.97$, $r^2 = 0.997$, $P < 0.001$, $n = 47$), and for older chicks (19 to 27 days),

$$\text{TBW} = 15.79 + 0.491 M \quad (3)$$

($\text{SE} = 1.91$, $r^2 = 0.842$, $P < 0.001$; $n = 35$).

Dovekie chicks do not drink; hence, water influx (W_i , ml/day) is from water in food (W_f , ml/day) and metabolic-water production (W_m , ml/day):

$$W_i = W_f + W_m. \quad (4)$$

The amount of water in the food equals the fresh mass of the food (M_f , g) times the fraction of water in the food (F_w , dimensionless):

$$W_f = M_f F_w. \quad (5)$$

The estimated metabolic-water production (water from food catabolism) was corrected for lipid and lean-dry-mass (mainly protein) change in growing tissues, assuming that the food fraction that is not catabolized but allocated toward body-mass growth yields no metabolic water. When body mass decreases, as in chicks near fledging (days 25–26), the correction adds the water from body-tissue catabolism.

$$W_m = M_f E_d E_a C - (\Delta M_l \cdot H_l + \Delta M_p \cdot H_p), \quad (6)$$

where E_d is energy density of fresh food (kJ/g), E_a is food assimilation efficiency (dimensionless), C is a conversion factor (ml $\text{H}_2\text{O}/\text{kJ}$ metabolized), ΔM_l and ΔM_p are tissue-lipid and protein mass changes (g/day), respectively, H_l and H_p are the metabolic-water yields (ml/g) of these tissues. The values used are: $F_w = 0.76$, $E_d = 6.75$ kJ/g, and $E_a = 0.80$ for Dovekie chicks' food (Taylor and Konarzewski 1992); $C = 0.026$ ml $\text{H}_2\text{O}/\text{kJ}$ (Schmidt-Nielsen 1990:333). Lipid and protein (lean dry mass) changes in growing chicks in 1986 and 1987 are from Taylor and Konarzewski (1989). H_l and H_p were assumed to be 1.07 and 0.50 ml $\text{H}_2\text{O}/\text{g}$, respectively (Schmidt-Nielsen 1990:333). The values from equations (5) and (6) were substituted in (4), and the latter was solved for food intake (M_f), which was converted to energy units.

To calculate water flux with the tritiated-water method, several assumptions are required (Nagy and Costa 1980). The most critical of these for growing animals is that tritium labels body water only. The incorporation of tritium into newly synthesized tissue would cause an overestimate of water-flux rates, because the specific activity of tritium in body water would decline owing to isotope binding as well as water influx, assuming that the binding occurs after the initial bleeding. If 10% of the decline in tritium-specific activity in our chicks during the 24 h after initial sampling was due to the incorporation of tritium, our values of water influx and food consumption might be overestimated by up to 16%. However, there are four reasons to expect that the values are not overestimated. First, the preliminary validation experiment by Gabrielsen et al. (1992) showed a very good agreement between food consumption calculated from water influx measured by the tritiated-water method and simultaneous direct determination of the amount of food consumed by Kittiwake (*Rissa tridactyla*) chicks. Second, two independent estimates of food consumption for the same Gentoo Penguin (*Pygoscelis papua*) chicks, derived from water- and sodium-influx rates (using tritiated water and ^{22}Na), were within 2% of each other (Robertson et al. 1988). Third, incorporation of tritium was estimated as only 0.1% of the total administered dose in nestling Glaucous-winged Gulls (*Larus glaucescens*; Hughes et al. 1987), and less than 2% in Chukar chicks (*Alectoris chukar*; J. B. Williams in Williams and Nagy 1985). Fourth, the

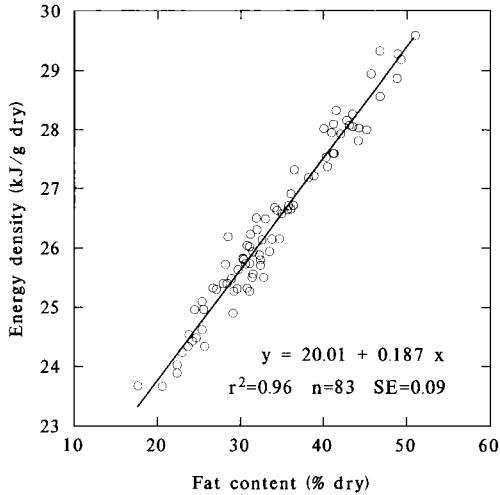


Fig. 1. Relationship between energy density and fat content in dry body mass in Dovekie chick. SE is standard error of estimate.

most convincing argument that our values of food consumption are not overestimated comes from the inspection of the Dovekie chick energy budget itself. The assimilated energy, calculated from food consumption via the tritiated-water method, is exactly equal to (and cannot be lower than) the sum of independently measured resting metabolic rate and the rate of energy accumulation in growing tissues at the age of maximum body-mass growth rate (i.e. when probability of tritium incorporation into newly synthesized tissue is highest).

The relationship between the chicks' body mass

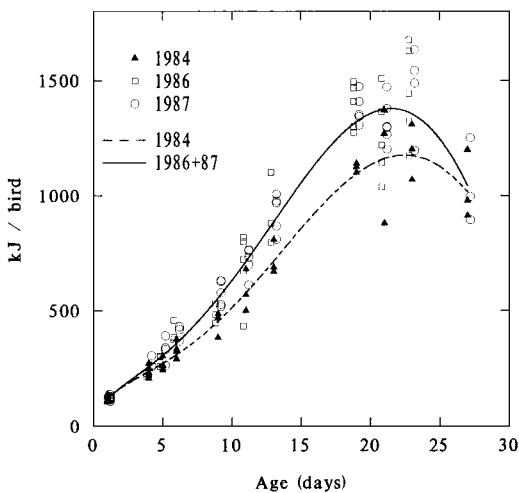


Fig. 2. Changes in energy content of Dovekie chicks with age. Relationships described with polynomials.

and age until the age of peak body mass was described by the Richards curve (Nedler 1962) fitted to the data using a weighted least-square method and the Marquardt algorithm (Bevington 1969). Richards growth curves were compared with an F-test (White and Brisbin 1980).

RESULTS

Energy content of tissues.—We found a highly significant dependence of energy density upon fat percentage in dry body mass of Dovekie chicks ($r^2 = 0.96$, Fig. 1). This enabled us to accurately estimate the energy density and, thus, total energy content of all 1986 and 1987 chicks.

Energy content of chicks differed among the three study years (Fig. 2). Energy content of 1984 chicks was significantly lower in the linear portion of its dependence on chicks' age (days 9 to 19) as revealed by ANCOVA followed by the Tukey test ($P < 0.05$). Energy contents of 1986 and 1987 chicks did not differ at these ages ($P > 0.05$). At the same time there were no differences among the slopes of three lines ($P > 0.10$). The maximum energy content, achieved on days 19 to 23 (the age of maximum body mass throughout nestling period) was also significantly lower in 1984 chicks than in 1986–1987, with no difference between 1986 and 1987 (ANOVA, Tukey test at $P = 0.05$). Lower energy content of 1984 chicks was due to lower fat content, as there was no difference in lean dry mass of chicks among years (Taylor and Konarzewski 1989). Energy contents of 1986 and 1987 chicks were lumped and used for further basic calculations of energy budget. Energy content of chicks decreased before fledging (Fig. 2) together with a decline in body mass and mass of fat (Taylor and Konarzewski 1989).

Metabolic rates.—Dovekie chicks are poikilothermic until day 5 (Konarzewski and Taylor unpubl. data). Body temperature in one- to five-day-old chicks measured immediately after their removal from the nest, usually from under a brooding parent, was $38.4 \pm \text{SD of } 0.7^\circ\text{C}$ ($n = 49$). The regression of body temperature on age was not significant ($P > 0.05$). There were no significant differences in body temperatures between chicks examined in the colony and used in metabolic trials on their first and third days of life (Table 1; t -test, $P > 0.05$). This means that air temperature in the metabolic chambers was similar to operative temperature experienced by young chicks during brooding. The conditions within the metabolic chamber also

TABLE 1. Body temperature, oxygen consumption, respiratory quotient (RQ), and thermal conductance in Dovekie chicks of various ages; means \pm SD. All parameters measured at ambient temperatures of 25° to 30°C in one-day-old chicks, at 25° in three-day-old chicks, and within range of 6° to 11° in older chicks.

Age (days)	<i>n</i>	Body mass (g)	Body temperature ^a (°C)	Oxygen consumption (mg/[g h])	RQ	Thermal conductance (ml O ₂ /[g h °C])
1	18	22.4 \pm 2.4	38.0 \pm 0.7	2.46 \pm 0.35	0.63 \pm 0.03	0.242 \pm 0.043 (115) ^b
3	15	31.6 \pm 3.8	38.9 \pm 0.4	3.11 \pm 0.35	0.69 \pm 0.03	0.225 \pm 0.024 (127)
7-10	14	69.8 \pm 9.3	39.2 \pm 0.5	4.38 \pm 0.25	0.71 \pm 0.02	0.145 \pm 0.010 (120)
13-15	19	103.2 \pm 14.7	39.7 \pm 0.3	3.86 \pm 0.25	0.74 \pm 0.04	0.124 \pm 0.010 (123)
20-22	17	124.6 \pm 13.1	39.7 \pm 0.3	3.06 \pm 0.27	0.75 \pm 0.02	0.100 \pm 0.008 (109)
25-27	12	115.3 \pm 9.8	39.8 \pm 0.3	3.13 \pm 0.29	0.69 \pm 0.05	0.100 \pm 0.011 (105)

^a Measured after metabolic trial.

^b Thermal conductance, as percent of value predicted from Aschoff's equation (1981) for adult nonpasserine birds of same body mass during activity time, given in parentheses.

approximated the natural thermal environment of older, homeothermic chicks. Dovekies nest in crevices in talus. The chick, even when not brooded, is well protected against wind and solar radiation.

Mass-specific resting metabolic rate peaked 7 to 10 days posthatch; then it declined considerably to days 20 to 22, and changed little up to fledging (Table 1). The respiratory quotient (RQ) averaged 0.74 in 7- to 22-day-old chicks and decreased in near-fledging chicks. Thermal conductance decreased continuously with age and dropped 60% between hatching and fledging (Table 1).

Metabolic rates and energy contents used for construction of energy budget were not measured in the same chicks, but body masses of chicks of these two groups did not differ. There was no difference between two Richards curves relating body mass to the age of chicks (up to the peak of body mass, day 21) fitted to the two data sets ($P > 0.20$). The parameters of the Richards growth curve fitted to the lumped data, as well as body masses of chicks in consecutive days, calculated from the curve, are given in the Appendix. Mean maximum growth rates, calculated as the instantaneous growth rate at the point of inflection (i.e. day 8) of the Richards curve (Nedler 1962, Hussell 1972) was 7.5 g/day, similar to that measured in other years in the same colony by other authors: 7.7 and 7.1 g/day in 1963-1964 and 1974-1975, respectively (Norderhaug 1980, Stempniewicz 1980).

Chicks' energy budget.—Resting metabolic rates reached maximum values on days 16 and 17 (Fig. 3). The rate of energy deposition in growing tissues calculated from the curve in Figure 2 (1986-1987) increased gradually after hatch-

ing, peaked only a few days earlier than resting metabolic rate, dropped in the next few days and became negative prior to fledging (Fig. 4). Thus, the sum of these two parameters, being the rate of resting energy assimilation (not including costs of activity of chicks) (A_r) reached its peak on day 14 (Fig. 4). This is exactly midway through the nestling period, as chicks fledged on average on the 27th day after hatching (Stempniewicz 1980, Konarzewski and Taylor unpubl. data). The energy deposited in tissues between days 1 and 21 (i.e. when deposition rate was positive) amounted to 1,254 kJ and constituted 29% of the A_r . The total A_r was 4,258 kJ by day 21.

We assumed that the cost of biosynthesis is one-third the rate of energy accumulation

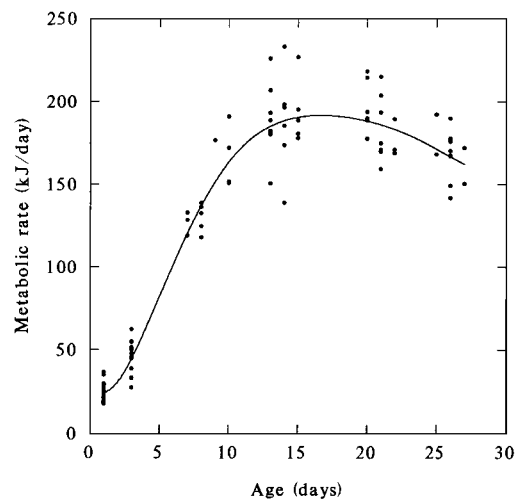


Fig. 3. Resting metabolic rate of Dovekie chicks as function of age. Curve is a polynomial. See Methods for ambient temperatures.

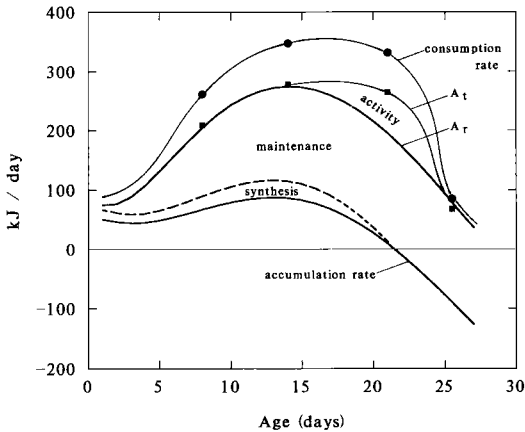


Fig. 4. Energy budget of a typical Dovekie chick. Circles represent energy consumed by chick as calculated from water-influx rates. Squares represent total energy-assimilation rate (A_t), calculated as the consumption rate multiplied by the assimilation coefficient. A_r is resting assimilation rate (not including activity costs), equal to resting metabolic rate plus accumulation rate. A_t is equal to A_r between days 1 and 15. Resting metabolic rate is partitioned into maintenance costs and costs of synthesis of body tissue.

(Ricklefs 1974). Maintenance energy is the resting metabolic rate minus the cost of biosynthesis. Maintenance energy constituted 60% of A_r over the chick's first 21 days of life.

Figure 4 also presents the energy consumed by chicks calculated from water-influx rates. In all age classes except fledglings, the water-influx rate was significantly correlated with body-mass change (Table 2). To unify energy consumed by chicks calculated from water influx with the data on resting metabolic rates and energy content of tissues, we used body-

mass change in chicks derived from the Richards growth curve mentioned above. These body-mass changes in chicks and regressions in Table 2 gave adjusted water-influx rates in chicks as a basis for calculation of food consumption (Table 2). The maximum rate of energy consumption occurred at the same age as did the maximum A_r , at the midpoint of the fledging period (Fig. 4, Table 2). The abrupt drop in consumption after day 21, accompanied by a recession in body mass and energy content of tissues (Fig. 2) is caused by cessation of chick feeding by the female parent; the chick is fed only by the male at that time (Taylor and Konarzewski in prep.).

We also estimated the total assimilated energy (A_t ; Fig. 4) by multiplying energy consumed by 0.80, the energy assimilation efficiency in Dovekie chicks (Taylor and Konarzewski 1992). The energy deposited in tissues up to day 21 constituted 26% of the A_t at that time. The difference between A_t and A_r is approximately the energy expended in activity. The estimated costs of activity were negligible over the first half of the nest period and attained 32% of A_r (48% of resting metabolic rate) in 21-day-old chicks (Fig. 4).

The mean maximum body-mass growth rate was 6.7 g/day in 1984, 11% less than in 1986–1987, and the two growth curves differed significantly ($P < 0.01$). The total energy deposited in tissues by the chick between 1 and 21 days of age in 1984 (calculated from lower curve in Fig. 2) was 17% lower than in 1986–1987.

DISCUSSION

Energy budget of chick.—A comparison of the rates of energy assimilation minus the costs of activity (A_r) in seabird chicks of similar body

TABLE 2. Water influx rates and estimated food consumption of Dovekie chicks.

Age (days) ^a	Mean body mass (g)	Water influx (WI, ml/day) vs. body-mass change (BMC, g/day)					Adjusted water influx ^d (ml/day)	Food consumption	
		Equation	P^c	r^2	SE	n		g/day	kJ/day
7–9	67.9 ± 6.8 (10)	WI = 24.0 + 1.235 BMC	0.01	0.37	10.0	17	33.2	38.8	262
13–15	94.7 ± 8.6 (9)	WI = 37.9 + 1.290 BMC	0.0001	0.68	13.0	18	44.7	51.5	348
20–22	126.1 ± 9.3 (9)	WI = 45.2 + 0.848 BMC	0.005	0.44	12.8	18	44.3	49.2	332
25–26	118.5 ± 8.7 (10)	WI = 13.7 ^e			1.2	10	13.7	12.7	86

^a 20–22 days is age of peak body mass in nest; Dovekie chicks fledge on average on day 27 after hatching.

^b n is number of chicks.

^c Significance level of regression slope (t -test).

^d See text.

^e Mean value; regression not significant ($P > 0.4$).

mass reveals that A_r of Dovekie chicks is one of the highest (Fig. 5A). This can be partially attributed to their very high cost of growth (energy-accumulation rate in growing tissues plus cost of biosynthesis), the highest among all species shown in Figure 5, which results from the combination of a rather high body-mass growth rate and high rate of fat deposition. Of the total accumulated energy in Dovekie chicks between days 1 and 21, 58% is in the form of fat (Taylor and Konarzewski 1989).

The high cost of maintenance similarly contributes to high A_r and to interspecific differences (Fig. 5B). Maintenance costs comprise "basal" costs (within thermoneutral zone), the costs of thermoregulation, and the calorogenic effect of food. High costs of thermoregulation in Dovekie chicks may be one of the causes of their high maintenance costs, as air temperatures in Dovekie nest crevices during chick development range between 3.6° and 11.1°C (mean = 6.5°; Konarzewski and Taylor 1989). The high costs of maintenance in Dovekie chicks are not caused by the poor insulative value of their down; thermal conductance of homeothermic chicks was not higher than 123% of the minimal conductance of adult nonpasserine birds of the same body mass (Table 2), and the conductance we obtained in our chicks was not always minimal. Different costs of thermoregulation alone cannot explain the differences in cost of maintenance in chicks shown in Figure 5B. Chicks of the two species of diving-petrel have much lower costs of maintenance, despite living in similar ambient temperatures (Roby 1991). Moreover, costs of thermoregulation might be of limited significance even in small polar birds, as they accounted for only 30% of maintenance costs in Arctic Tern chicks (Klaassen et al. 1989). On the other hand, estimated maintenance costs are lower in Least Auklet chicks than in the closely related Dovekie due to the correction for parental brooding made for Least Auklet chicks even close to fledging when calculating their energy budget (Roby 1991). Brooding was considered in Dovekie chicks only when younger than seven days (Norderhaug 1980). Even fledgling Least Auklet nestlings are attended by parents at night, while Dovekie chicks are fed 24 h a day in continuous light of Arctic summer (Stempniewicz and Jezierski 1987). It is also possible that presumably high metabolic rates in thermoneutrality bring about high cost of maintenance in Dovekie chicks. Basal met-

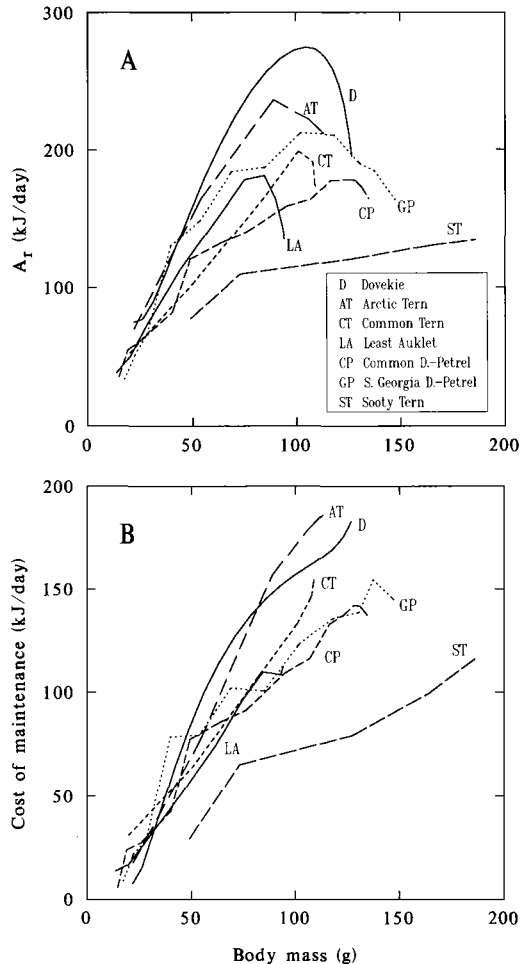


Fig. 5. Energy expenditures of Dovekie chicks and other seabird chicks of similar body mass: Arctic Tern (*Sterna paradisaea*; Klaassen et al. 1989); Common Tern (*S. hirundo*) and Sooty Tern (*S. fuscata*; Ricklefs and White 1981); Least Auklet (*Aethia pusilla*), South Georgia Diving-Petrel (*Pelecanoides georgicus*), and Common Diving-Petrel (*P. urinatrix*; Roby 1991). (A) Rates of resting energy assimilation (A_r ; see Fig. 4 and text for definition); (B) Costs of maintenance (resting metabolic rate minus cost of biosynthesis).

abolic rates of adult birds from high latitudes generally exceed those of species from lower latitudes (Weathers 1979). The basal metabolic rates of adult Dovekies are equal to 212% of the rate expected for bird species of the same body mass (Gabrielsen et al. 1991), while the same figures in adult Least Auklets, South Georgia Diving-Petrels, and Common Diving-Petrels are 191, 156, and 150%, respectively (Roby and Ricklefs 1986). Klaassen and Drent (1991) also

showed a positive correlation between resting metabolic rates in hatchlings and latitude.

Energy expended on activity is rather small in Dovekie chicks when compared with that expended by other bird species (Dunn 1980), as the chicks usually remain inactive in their nest crevices (pers. observ.). The highest estimated costs of activity, which occur on about day 21, result from chicks exercising their wings at the entrance of the crevice, an activity that starts at the age of 15 days (Stempniewicz 1981, and our own observations). Despite low activity costs, the consumed and assimilated energy is relatively high; the peak assimilated energy (maximum A_1) is 31% higher than that predicted for a chick of the same mass and age at fledging (from equation 14 by Weathers 1992).

The difference between Dovekie-chick energy requirements (measured in absolute values) and those of other seabird chicks is greatest at older ages (Fig. 5A). This large difference may contribute to the fact that, in contrast to all other species shown in Figure 5, Dovekie chicks attain only 65 to 70% of adult mass at fledging. High maintenance costs that increase with age (Fig. 5B) and appearance of activity costs at older age in Dovekie chicks (Fig. 4), combined with a high energy cost of foraging in adult Dovekies (see next section), may explain the arrest in growth of Dovekie chicks well before attaining adult body mass. At the age of maximum growth and maximum consumption (day 14, Fig. 4), the chicks ingest 5.9 g protein/day (as calculated from composition of their food; Taylor and Konarzewski 1992), and they accumulate 1.7 g lean dry mass (mainly protein) per day (Taylor and Konarzewski 1989). At the same time the amount of fat ingested (4.5 g/day = 178 kJ/day) is sufficient to meet combined costs of maintenance and biosynthesis (188 kJ/day). The dietary surplus of protein may be metabolized to meet maintenance costs, and the energy saved may be stored as fat. At that age growth of chicks is not limited by the amount of energy or by protein delivered by parents. After day 14 further increase in metabolic costs with no increase in energy consumed is accompanied by a slowing down of the rate of increase in body mass, until it reaches zero on day 21 (Fig. 4).

Taking into account the relatively high metabolic rates of Dovekie chicks, it might be expected that the chicks are vulnerable to food shortages (e.g. during inclement weather). In fact, there was significant correlation between

several weather parameters and body mass in 1984 chicks at the age of their maximum energy requirements (Konarzewski and Taylor 1989). In 1984 chicks, an obvious reduced rate of increase or even a decline in the relative amount of fat was observed at the beginning of the period of peak energy requirements; also, the fat contents, energy densities, and body masses of older 1984 chicks were significantly lower than in 1986 and 1987 (Fig. 2; Taylor and Konarzewski 1989) resulting in lower total energy deposited in tissues by the age of peak body mass (Fig. 2). All were linked with unfavorable weather in the Hornsund area in 1984. Nevertheless, this does not indicate that Dovekie chicks suffer food shortages, as all individuals measured in the three seasons had a substantial surplus of fat and the interfeed intervals were not unusually long (Taylor and Konarzewski 1989).

Comparison of energy requirements of chick and adult.—High chick energy demands might be expected to contribute to very high energy expenditures of feeding parents. However, the energy delivered to the chick by one parent is only 15% of the energy gathered by the parent to meet both its own and its chick's requirements (Table 3). This calculation is based on the period between days 8 and 21, when the chick is no longer brooded by its parents and is still fed by both parents (Taylor and Konarzewski in prep.). Parents do not share equally in feeding over this time; 64% of meals are delivered to the chick by the female (Taylor and Konarzewski in prep.). The average adult field metabolic rate (FMR) used for calculation included both sexes and was a mean weighted for feeding frequency, as the capture of birds feeding their chicks for FMR determination was proportional to their individual feeding frequency (Gabrielsen et al. 1991). Because there is no difference in food load mass and food composition between sexes (Taylor and Konarzewski in prep.), and adult FMR should be proportional to the number of foraging trips, the ratio should be close to 15% for both sexes.

The proportion of total energy gathered by parents that is delivered to the chick is similar in the other alcid studied, the Least Auklet, and in two species of diving-petrels (Table 3). Roby and Ricklefs (1986) noted that the proportion of energy delivered by European Starlings to their five-chick brood was three to four times higher than that in Least Auklets and diving-

TABLE 3. Proportion of energy gathered by alcids, diving-petrels and European Starlings delivered to their chicks during period of peak chick food demands.^a

Species	Adult body mass (g)	Brood size	Adult FMR ^b (ml CO ₂ /[g h])	Adult energy consumption ^c (kJ/day; A)	Food delivered to chicks (kJ/[adult day]; B)	Proportion of energy delivered to chicks (%; 100 B/[A + B])
1 European Starling (<i>Sturnus vulgaris</i>)	76	5	6.18	450	460	50
2 Least Auklet (<i>Aethia pusilla</i>)	84	1	6.69	465	97	17
3 South Georgia Diving-Petrel (<i>Pelecanoides georgicus</i>)	109	1	6.53	602	123	17
4 Common Diving-Petrel (<i>P. urinatrix exsul</i>)	137	1	6.34	723	101	12
5 Dovekie (<i>Alle alle</i>)	164	1	6.68	904	162	15
6 Black Guillemot (<i>Cepphus grylle</i>)	381	2	3.63	1121	525	32

^a Sources: (1) Ricklefs and Williams (1984), Westerterp (1973); (2,3,4) Roby and Ricklefs (1986), Roby (1991); (5) Gabrielsen et al. (1991), present study; (6) F. Mehlum, G. W. Gabrielsen and K. A. Nagy (unpubl. data), Asbirk (1979; chicks' food consumption), Cairns (1987; energy density of food).

^b Field metabolic rates in birds feeding chicks measured by doubly-labeled-water method.

^c Calculated from FMR, assuming 0.67 energy-assimilation coefficient in European Starlings (Ricklefs and Williams 1984) and 0.77 in all others (Jackson 1986, Davis et al. 1989).

petrels rearing a single chick, although mass-specific field metabolic rates and body masses of all these birds were similar (Table 3). This means that seabirds are less efficient at delivering energy to the nest per unit energy expended. These authors suggested that one-chick broods of auklets and diving-petrels are a consequence of the high energy costs of foraging and transporting chick meals.

The case of the Dovekie supports this supposition, especially as its mass-specific field metabolic rate while feeding chicks is the highest among all birds mentioned above, despite its larger body mass (Table 3). In another study (Gabrielsen et al. 1991), we associated high metabolic costs of adult Dovekies with high costs of flight and their off-shore mode of foraging. Foraging Dovekies are observed as far as 150 km from the colonies (Byrkjedal et al. 1974, Brown 1976, but see Hartley and Fisher 1936). Both auks and diving-petrels utilize their wings for flying and propulsion under water. The latter is associated with strong selection for small wings and very high wing loading (i.e. ratio of body mass to wing area; Warham 1977, Pennyquick 1988), which in turn increases the energy cost of flying. The Black Guillemot, an alcid that usually raises two chicks, is able to collect more food. The proportion of energy delivered to chicks by Black Guillemots is twice that of Dovekies, despite a much larger body mass of

the former species (Table 3); the proportion of acquired food that is allocated to a single nestling should decrease with an increase in body mass of the parent (Walsberg 1983). However, Black Guillemots always obtain food for chicks inshore in shallow water (Asbirk 1979, Cairns 1987). The proportion of energy delivered to chicks by Black Guillemots is even higher than that given in Table 3 when calculated using chick food consumption rates reported by Cairns (1987) and/or field metabolic rates of adult birds measured by Gaston et al. (in Roby and Ricklefs 1986). The proportion of energy delivered to chicks by Dovekies is very similar to that in the Least Auklet (higher food consumption in Dovekie chicks is associated with higher consumption in adults; Table 3). However, Least Auklet chicks attain 108% of adult body mass at fledging (Roby and Brink 1986), while Dovekies fledge at only 65 to 70% of adult body mass, although at the same age (Norderhaug 1980, Stempniewicz 1980, Konarzewski and Taylor 1989). This difference in the growth pattern also may be associated with foraging range, as Least Auklets normally forage within 5 to 10 km of the colony (Hunt et al. 1978).

Summarizing, we suggest that the low allocation to chicks of the total food collected by adult Dovekies reflects the adults' high cost of foraging (unproductive time and energy expended to fly between breeding colony and dis-

tant foraging areas, combined with high cost of flight itself). In addition, high chick demands at older ages may contribute to the high energy expenditures of adults. This may explain in large part the restriction of Dovekie brood size to one chick and the relatively low chick mass at fledging compared with adult mass.

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APPENDIX. Parameters of Dovekie chick's energy budget.

Age (days)	Body mass (g) ^a	Energy content (kJ) ^b	Increment in tissue energy (kJ/day) ^c	Resting metabolic rate (kJ/day) ^d
1	21.9	123.6	50.3	24.5
2	26.1	172.4	46.4	30.7
3	31.0	217.4	44.4	44.4
4	36.5	262.1	45.7	62.3
5	42.6	309.4	49.4	82.1
6	49.2	361.3	54.7	102.0
7	56.3	419.1	61.0	120.7
8	63.7	483.4	67.6	137.4
9	71.2	554.2	73.9	151.8
10	78.7	631.1	79.5	163.6
11	85.9	712.9	83.9	173.0
12	92.6	798.5	86.7	180.1
13	98.9	885.8	87.6	185.2
14	104.5	973.1	86.3	188.6
15	109.4	1,058.0	82.8	190.6
16	113.7	1,138.0	76.7	191.6
17	117.3	1,210.7	68.1	191.7
18	120.3	1,273.6	57.0	191.1
19	122.9	1,324.1	43.4	189.9
20	124.9	1,359.9	27.5	188.2
21	126.6	1,378.6	9.4	185.9
22		1,378.2	-10.5	183.1
23		1,357.0	-32.1	179.7
24		1,313.6	-54.9	175.7
25		1,247.0	-78.5	171.2
26		1,156.6	-102.3	166.5
27		1,042.5	-125.8	162.1

^a Calculated from Richards growth curve

$$W(t) = A / (1 + \lambda \exp[-k(t - t_i)]^{1/\lambda})$$

where A is asymptote, k is growth rate, t is age, t_i is inflection point, and λ is factor determining shape of growth curve. Values were: A of 133.5; k of 0.236; t_i of 8.66; and λ of 1.154.

^b From the 1986-1987 curve in Figure 2.

^c For example, value for day 15 calculated as day 15.5 minus day 14.5

^d From curve in Figure 3.