DIET AND POSTNATAL ENERGETICS IN CONVERGENT TAXA OF PLANKTON-FEEDING SEABIRDS

DANIEL D. ROBY[1]

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

ABSTRACT.—To evaluate the influence of diet composition on seabird postnatal development, I examined the relationships between feeding rate, energy intake, energy partitioning, and chick growth in three species of high latitude, plankton-feeding seabirds: Least Auklet (*Aethia pusilla*), South Georgia Diving Petrel (*Pelecanoides georgicus*), and Common Diving Petrel (*P. urinatrix*). Average dietary lipid content varied from 22 to 46% of dry mass among the three species. Least Auklet chicks were fed meals rich in wax esters; on average 63% of total energy intake was in the form of wax. Interspecific comparisons of chick dietary composition and energy budgets indicated that calanoid copepods, a wax ester-rich food, was a balanced source of protein and lipids. However, the lipid content of Antarctic krill (*Euphausia superba*) was insufficient to meet maintenance energy requirements of Common Diving Petrels. Lipid-rich diets were associated with shorter brooding periods, higher rates of nestling fat deposition, and larger lipid reserves at fledging. Accumulation rates of lipid-free dry matter were similar in the three species despite differences in energy intake related to diet. The energy cost of growth was a relatively minor component of nestling energy budgets; most assimilated energy was allocated toward maintenance and fat deposition. Selection apparently favors high latitude seabirds that meet the high energy requirements of their chicks by providing a lipid-rich diet. Differences in diet composition explained much of the variation in postnatal development among the three species, but there was no evidence that energy limited growth per se. *Received 11 December 1989, accepted 30 July 1990.*

PELAGIC seabirds share a suite of life history traits that includes single chick broods, slow growth, and long development periods (Lack 1968). These reproductive traits have been attributed to limitations in providing food to the chick. Lack (1968) inferred that the reproductive pattern in seabirds serves to reduce energy requirements at the nest to a level that a breeding pair can consistently meet. Researchers assumed that the availability of energy to a breeding pair is constrained by both the scarcity and the unpredictability of potential prey at sea (Ashmole 1963, 1971; Harris 1977; Nelson 1977; Case 1978). Energy limitation is viewed as a pervasive force selecting for observed patterns in seabird reproduction (Drent and Daan 1980).

Much of the variation in post-hatching developmental patterns in the seabird family Alcidae is apparently a consequence of differences in feeding ecology (Sealy 1973). Species that forage farther offshore and feed their young less frequently have slower growth rates, deposit larger fat reserves, and fledge before they attain adult mass. Ricklefs and White (1981) showed that growth in the oceanic Sooty Tern (*Sterna fuscata*) is slower than growth in the nearshore-feeding Common Tern (*S. hirundo*), and that daily energy requirements of Sooty Tern chicks peak at a lower level than those of the Common Tern. Also, the lipid reserves of Sooty Tern chicks were approximately 4 times greater than those of Common Terns, which is consistent with longer fasting periods for the young of the offshore species. These results suggest that the slower growth and larger fat depots of Sooty Tern chicks are related to low and variable rates of energy provisioning.

Ricklefs and White (1981) estimated that doubling the growth rate (accumulation of lipid-free dry matter) of Sooty Tern chicks would result in only a 20% increase in total energy requirements of the chick and only a 5% increase in adult energy requirements. They concluded that energy could not limit growth rate in this species. Similarly, in a study of the energetics of slow growth in Leach's Storm-Petrel (*Oceanodroma leucorhoa*), Ricklefs et al. (1980a) estimated that the accumulation of lipid-free dry matter (LFDM) amounted to <5% of the

total daily energy requirement. The energy equivalent of daily lipid deposition was 3–8 times that of LFDM, indicating that variation in growth rate would be expected to have little affect on total energy requirements of the nestling. The regularity in feeding of Leach's Storm-Petrel chicks implies that the large lipid reserves of nestlings are not an adaptation to survive fasts (Ricklefs et al. 1985), but instead they may represent an "energy sink" for chicks fed lipid-rich but protein-poor diets (Ricklefs 1979). These findings contradict the hypothesis that slow growth in offshore-feeding seabirds is an adaptation for reducing energy requirements at the nest and imply that other factors are responsible for long development periods. Ricklefs (1979, 1983) has made a strong case for constraints at the tissue level as the primary factor limiting growth in semiprecocial seabird chicks.

Studies of the relationship of diet to seabird development have emphasized the quantity of food fed to chicks. Little attention has been paid to variation in the quality of chick diets, yet the biochemical composition of seabird prey varies considerably (Clarke and Prince 1980, Ricketts and Prince 1981, Prince 1985). Analyses of high-latitude zooplankton indicate large variation in lipid content (Lee et al. 1972, Benson and Lee 1975). Lipids constitute up to 77% of dry mass in some zooplankters (Lee 1974), which implies that certain zooplankton diets may be energy-rich but protein-deficient. Considering the variability in composition of high-latitude zooplankton, prey selection by adult plankton-feeding seabirds may have important consequences for chick energy intake and the partitioning of assimilated energy among competing functions of maintenance, growth, and fat deposition.

If seabird growth is largely energy limited, and interspecific dietary differences result in significant variation in diet quality, then much of the variation in seabird postnatal development would be a function of diet composition. Specifically, seabird chicks with relatively high lipid diets would grow faster and fledge at a younger age. Conversely, if chick growth is constrained by factors that operate at the tissue level, differences in diet composition should bear little on development. High-lipid diets would be reflected in higher rates of lipid deposition by chicks, but not higher growth rates and shorter nestling periods.

I gathered data on chick meal sizes, feeding frequency, and diet composition for three species of high latitude, plankton-feeding seabirds. The three species are from two convergent taxa: auklets (Charadriiformes: Alcidae) and diving petrels (Procellariiformes: Pelecanoididae). All three are plankton-feeders that capture prey by pursuit-diving (sensu Ashmole 1971), yet taxonomic composition of the diet differs considerably (Bédard 1969, Payne and Prince 1979). I describe the energy requirements of chicks and how those requirements are partitioned among maintenance, growth, and lipid deposition functions throughout the nestling period. I compared the composition of chick diets with the patterns of energy allocation among the three species to test the hypothesis that differences in postnatal development relate to diet.

METHODS AND MATERIALS

I studied Least Auklets on St. George Island (56°35′N, 169°35′W) in the Pribilof Islands, Alaska, from June to August, 1981 and 1982. Nests were located and marked in a large (ca. 129,000 breeding individuals; Hickey and Craighead 1977) colony on the slopes of Ulakaia Hill. The study area was described in detail by Roby and Brink (1986a, b). Work on diving petrels was conducted on Bird Island (54°00′S, 38°02′W), located at the western end of South Georgia, during January and February 1982. Locations of study colonies are described in Roby and Ricklefs (1983). Nest burrows and nesting habitats of the two diving petrel species are described by Payne and Prince (1979).

Nests were checked daily during the hatching period to determine the date of hatching, and known-age chicks were periodically weighed and wing chord measured during the nestling period. A series of known-age chicks, in approximately equally spaced age classes from hatching to fledging, were removed from their nests around midday. The actual date of hatching was known for only a few Common Diving Petrel chicks, so age was estimated early in the nestling period from the relationship of wing length to age (Payne and Prince 1979). Chicks were transported to field laboratories where metabolic trials were conducted. Oxygen consumption was measured volumetrically using a temperature-controlled, closed system (Ricklefs and Roby 1983). Chicks were weighed at the beginning and end of each respirometry trial on an Ohaus triple beam balance (±0.1 g). Oxygen consumption rates were converted to $cm^3 \cdot g^{-1} \cdot h^{-1}$ by dividing by the mass of the subject at the beginning of the trial.

After respirometry trials, subjects were humanely sacrificed by thoracic compression, placed in plastic bags, and frozen at −20°C for later determination of

body composition. After partial thawing, each carcass was plucked, skinned, and dissected into 15 body parts. Feathers, skin, and body parts were placed in separate preweighed aluminum pans and immediately weighed on a Sartorious Model 2463 electronic balance (±0.001 g) to determine wet mass. Then each component was oven-dried to constant mass at 50–60°C. The dried skin and body parts were wrapped separately in cotton gauze, and extracted for 48 h in each of three baths of 5:1 (v/v) petroleum ether and chloroform. This solvent system removes storage lipids (triacylglycerols) and structural lipids (phospholipids), but very little nonlipid material (Hagan et al. 1967, Dobush et al. 1985). In the case of fatty carcasses, it was sometimes necessary to increase the number of successive baths to as many as six before achieving constant mass. Following extraction, carcasses were oven-dried at 50–60°C for 24 h to evaporate solvents, and reweighed to determine mass of lipid-free dry matter (LFDM). Lipid mass was determined by subtraction.

I estimated rates of accumulation of LFDM (including skin and plumage) and lipid during the nestling period for each species from changes in chick body composition as a function of age. Growth was defined as accumulation of LFDM and did not include accumulation of lipid. Data on age-specific total body mass, LFDM mass, and lipid mass were each fitted to linear, quadratic, cubic, logistic, and Gompertz models using procedures in the SAS package (SAS Institute, Inc., 1982). The model that minimized the residual mean square was used to estimate the rate of accumulation of LFDM or lipid during each phase of the nestling period. The predicted values from each model were compared with the actual measurements to check for biases in the distribution of residuals.

To estimate energy expenditure rates of chicks, I multiplied the average mass-specific rate of oxygen consumption at each age times the average body mass at that age (Roby and Brink 1986a; Roby and Ricklefs unpubl. data). These oxygen consumption rates were adjusted for age-specific differences in the incidence of brooding. I assumed that, when brooded by their parents, chicks were within the thermal neutral zone and consumed oxygen at standard metabolic rate (SMR). Standard metabolic rate for each chick was assumed to be the minimum oxygen consumption rate recorded during metabolic trials. I also assumed that unattended chicks were exposed to average ambient temperatures recorded in nest sites (7.8°C for Least Auklets, 8.8°C for South Georgia Diving Petrels, 7.0°C for Common Diving Petrels). Oxygen consumption rates at these ambient temperatures were estimated from the average of rates measured at 5°C and 10°C. I assumed that diving petrel chicks were at SMR continuously until 6.5 days (South Georgia Diving Petrel) or 11 days (Common Diving Petrel) post-hatch, the average length of their respective brooding periods (Roby and Ricklefs 1983). Subsequently, I as-

sumed diving petrel chicks maintained SMR for 4 h each day when adults were normally in attendance during the night. Least Auklet chicks were brooded continuously until 4 days post-hatch and then intermittently during the day until 18 days post-hatch (Roby and Brink 1986a). I used data on age-specific brooding frequency of Least Auklet chicks to estimate the proportion of the day at standard metabolic rate and I assumed that all chicks, regardless of age, were at SMR during the night, when both parents were normally in attendance. I made no attempt to incorporate potential energy costs of activity into estimates of daily respired energy. Such costs are likely to be insignificant until nestlings begin to exercise their wings just before fledging. The energy equivalent of oxygen was assumed to be 20.1 kJ/l O_2 consumed (Ricklefs 1974).

I calculated the energy equivalent of growth during each phase of the nestling period from the energy equivalent of accumulated LFDM plus the estimated cost of LFDM biosynthesis. I calculated the energy equivalent of lipid deposition from the energy equivalent of accumulated lipids plus the estimated cost of adipose tissue biosynthesis. I assumed the following combustible energy equivalents of accumulated tissue: LFDM (includes protein, carbohydrate, and skeletal tissue) = 20.5 kJ/g; lipid = 37.7 kJ/g (Ricklefs 1974). Biosynthesis was estimated as 0.33 times the energy equivalent of accumulated tissue (Ricklefs 1974). I calculated the energy expended for maintenance by subtracting the total energy cost of biosynthesis (LFDM + lipid) from the energy equivalent of oxygen consumption. Total energy requirement was the sum of growth, lipid deposition, and maintenance requirements.

The frequency of chick feeding in Least Auklets was measured by continuous observation of a small colony of marked adults (Roby and Brink 1986a), while feeding frequency of diving petrels was determined by an overnight weighing technique (Roby 1989). I estimated daily food intake of chicks from the product of average frequency of meal delivery × average chick meal mass. Chick meals from all three species were collected by mist-netting adults as they returned to the colony to feed chicks. In the laboratory, the lipid content of chick meals as a percentage of wet mass was determined by the extraction and quantification of lipid classes (wax esters, triacylglycerols, free fatty acids, phospholipids) from a subsample of chick meals (n = 14 Least Auklet meals, n = 12 each South Georgia and Common diving petrel meals) by methods described by Roby et al. (1986). A second subsample of chick meals (n = 12 Least Auklet, n = 6 each South Georgia and Common diving petrel) was oven-dried to constant mass at 50–60°C to determine water content. Average LFDM content was determined by subtracting average lipid content and average water content from average wet mass. Protein content was determined for the chick meals that were dried to

determine water content. Following extraction of lipids from the dried meals, total nitrogen content was determined by the Kjeldahl method at the Forage Analysis Laboratory, New Bolton Center, University of Pennsylvania. I estimated rates of lipid, LFDM, and protein intake (g/day) for each species from their average proportions in chick meals (% of wet mass) times the average rate of food intake (g wet mass/day).

Carbohydrate, chitin, and ash contents of chick meals were not measured and were estimated from published values. Carbohydrate is a minor constituent in planktonic crustacea. For *E. superba*, published values for carbohydrate are only 5% (Raymont et al. 1971) and 2.7% of LFDM (Clarke 1980). Ash was the major nonprotein constituent of LFDM: ash averaged 21.6% in three species of boreal euphausiids (Falk-Petersen 1981), and 19% and 18.3% in *E. superba* (Raymont et al. 1971 and Clarke 1980, respectively). Lipid-free dry matter in *E. superba* consisted of 5% chitin (Raymont et al. 1971) and 10.9% chitin (Clarke 1980). Clarke (1980) did not account for 11.4% of LFDM in *E. superba*, but it probably consisted primarily of free fatty acids and other metabolic breakdown products. For purposes of estimating the energy content of chick diets, I used the average of published values to estimate the composition of nonprotein LFDM: 52% ash, 19% chitin, and 10% carbohydrate. I assumed that the unidentified portion of LFDM had the same energy content as protein.

Chitin is generally considered an indigestible component of the diet, but there is growing evidence that among birds in general, and seabirds in particular, at least a portion of dietary chitin is metabolized (Jeuniaux and Cornelius 1978, Stemmler et al. 1984). Although digestive efficiencies for chitin have been measured at 40–60% (A. R. Place pers. comm.), for the purpose of estimating energy content of seabird diets I assumed that chitin was digested completely. To estimate the energy content of the diet, I assumed the following gross energy equivalents: lipid = 39.5 kJ/g, protein = 18.0 kJ/g, carbohydrate = 17.3 kJ/g (Ricklefs 1974), chitin = 17.2 kJ/g (Clarke 1980).

RESULTS

Nestling diets.—Parents of the three study species must supply all the prefledging nutritional requirements of their nestlings. Least Auklets are only active at the nesting colony during the day while diving petrels are strictly nocturnal. Short nights at high latitudes have important consequences for chick feeding frequency in nocturnal seabirds. Least Auklet chicks were fed an average of 5.6 meals each day, while diving petrel chicks were fed at most two meals each night, one from each parent (Table 1). In diving petrels and other nocturnal seabirds,

larger meal size compensates for lower frequency of meal delivery. The average daily food intake was lowest in Least Auklets (Table 1). Daily food intake of chicks as a percentage of adult mass was 42% in Least Auklets, 37% in South Georgia Diving Petrels, and 33% in Common Diving Petrels (Table 1).

The taxonomic composition of chick meals differed among the three species, and the biochemical composition of chick diets reflected those differences (Table 2). The Least Auklet diet was dominated by calanoid copepods (95% of meal volume on average). South Georgia Diving Petrel chick meals were dominated by the euphausiids *Thysanoessa* sp. (63%) and *Euphausia superba* (26%). Common Diving Petrel chick meals were dominated by *E. superba* (78%) with copepods second in importance. Because of the preponderance of calanoid copepods, Least Auklet meals had significantly higher lipid content ($t = 3.36$, $P < 0.05$), and most of the lipid was in the form of wax esters (Table 2). Chick meals of Common Diving Petrels consisted mostly of *E. superba* and had significantly lower lipid content ($t = 5.43$, $P < 0.05$) and little wax. Associated with the preponderance of euphausiids in the diet, South Georgia and Common diving petrel meals had significantly higher protein levels than Least Auklet meals ($t = 10.20$, $P < 0.05$). South Georgia Diving Petrel meals had relatively high average lipid content in addition to high protein content, apparently because the main dietary item (*Thysanoessa*) had larger lipid stores than *E. superba*. The preponderance of *Thysanoessa* sp. in the chick meals of South Georgia Diving Petrels and their absence in Common Diving Petrel meals may be a consequence of differences in either selectivity or availability. Common Diving Petrels nest earlier than South Georgia Diving Petrels on Bird Island, and although it is unlikely that *E. superba* is less available when South Georgia Diving Petrels raise their young, it is possible that *Thysanoessa* is scarce during the chick-rearing period of Common Diving Petrels.

Differences in lipid and protein content of meals resulted in differences in the energy density of chick diets. The average energy densities of Least Auklet (5.48 kJ/g wet mass) and South Georgia Diving Petrel chick (5.77 kJ/g) diets were similar. In Common Diving Petrels, energy density was significantly lower (4.16 kJ/g wet mass, $t = 4.294$, $P < 0.05$). The average energy density of Common Diving Petrel meals

TABLE 1. Average food intake for Least Auklet, South Georgia Diving Petrel, and Common Diving Petrel chicks. Means are ±SD; sample sizes are in parentheses.

	Least Auklet	South Georgia Diving Petrel	Common Diving Petrel
Adult mass (g)	84.5 ± 5.23 (44)	115.3 ± 6.99 (24)	145.0 ± 6.85 (32)
Peak chick mass (g)	91.5 ± 11.67 (11)	142.0 ± 15.71 (52)	134.0 ± 13.75 (124)
% of adult mass	108.3	123.1	92.4
Feeding frequency (meals/day)	5.60 ± 1.08 (10)	1.83 ± 0.38 (78)	1.90 ± 0.35 (78)
Chick meal mass (g)	6.30 ± 2.27 (28)	23.3 ± 3.92 (24)	25.5 ± 4.54 (32)
% of adult mass	7.5	20.2	17.6
Food Intake (g/day)	35.3 ± 14.42	42.6 ± 11.39	48.5 ± 12.41

was within the range of values reported for fresh *E. superba* (3.8–5.5 kJ/g; Clarke and Prince 1980). Of the total estimated energy content of chick diets, lipid contributed 69% in Least Auklet meals, 60% in South Georgia Diving Petrel meals, and 43% in Common Diving Petrel meals.

Chick growth.—Logistic models had the lowest residual mean square when fitted to data on total body mass as a function of age for each of the study species (Table 3). The logistic growth rate constant (K) was significantly greater and the inflection point (I) and asymptote (A) significantly less for Least Auklets compared with the two diving petrel species (no overlap in 95% confidence limits). For the two diving petrel species, K and I were not significantly different ($P > 0.05$), but the asymptote of the fitted logistic equation was significantly greater (no overlap in 95% confidence limits) for South Georgia Diving Petrels. Although these results suggest that Least Auklets grow more rapidly than either of the diving petrels, interspecific

differences in the contribution of lipid deposition to overall growth obscure the pattern of LFDM accumulation.

Of the five models used to fit data on LFDM as a function of age, logistic equations resulted in the lowest residual mean square for each species. The growth rate constant for the logistic equation fitted to LFDM data was highest in Least Auklets (smallest species) and lowest in Common Diving Petrels (largest species; Fig. 1, Table 3), but the 95% confidence limits about the value of K overlapped for the three species. Also, a trend of decreasing growth rate with increasing asymptotic mass is expected based on the allometric scaling of growth rate to body size described by Ricklefs (1979). Consequently, growth rate of LFDM was similar among the three study species once K values were adjusted for differences in adult body mass. The difference in the length of the nestling period between Least Auklets and the two diving petrels was primarily a function of differences in as-

TABLE 2. Average taxonomic composition (% volume) and biochemical composition of chick diets in three species of high latitude plankton-feeding seabirds. Means are ±SD; sample sizes are in parentheses.

	Least Auklet	South Georgia Diving Petrel	Common Diving Petrel
Taxonomic composition			
Calanoid copepods	94.8 ± 3.2 (12)	3.5 ± 11.5 (12)	21.0 ± 20.6 (12)
Euphausia superba	—	26.3 ± 37.5 (12)	78.0 ± 20.5 (12)
Thysanoessa sp.	2.4 ± 1.96 (12)	63.3 ± 32.5 (12)	0.1 ± 0.58 (12)
Other Taxa	2.8 ± 2.53 (12)	5.5 ± 7.0 (12)	1.4 ± 1.73 (12)
Biochemical composition			
Water[a]	78.6 ± 3.28 (12)	75.8 ± 1.00 (6)	79.4 ± 1.41 (6)
Total lipid[b]	45.5 ± 8.33 (14)	36.0 ± 6.02 (12)	21.7 ± 6.85 (12)
Wax esters[b]	39.0 ± 1.24 (6)	14.5 ± 6.76 (6)	5.4 ± 3.94 (6)
Protein[b]	34.1 ± 3.12 (12)	44.2 ± 1.01 (6)	52.2 ± 1.07 (6)
Chitin and carbohydrate[c]	6.2	5.8	7.3
Ash and unrecovered[c]	15.6	14.1	18.8

[a] Percent fresh mass.
[b] Percent of dry mass.
[c] Estimated from published values in the literature (see text).

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TABLE 3. Parameters of fitted equations for lipid-free dry matter (LFDM) mass and lipid mass as a function of age for nestlings of Least Auklet, South Georgia Diving Petrel, and Common Diving Petrel. Means are ±SE: K is the rate constant (days⁻¹), I is the inflection point (days), and A is the asymptote (g).

	Logistic parameter				
	K	I	A	r^2	Residual mean square
Least Auklet					
Total Mass	0.239 ± 0.007	8.6 ± 0.15	95.8 ± 1.07	0.990	32.69
Lipid	0.215 ± 0.039	14.5 ± 1.3	20.9 ± 1.8	0.964	5.49
LFDM	0.186 ± 0.012	11.4 ± 0.48	22.1 ± 0.63	0.996	0.84
South Georgia Diving Petrel					
Total Mass	0.145 ± 0.0036	14.9 ± 0.30	147.5 ± 1.93	0.985	73.38
Lipid	0.163 ± 0.031	19.3 ± 1.70	30.4 ± 2.16	0.969	11.69
LFDM	0.153 ± 0.011	16.3 ± 0.76	31.1 ± 0.94	0.994	2.61
Common Diving Petrel					
Total Mass	0.146 ± 0.0081	15.6 ± 0.37	138.5 ± 1.71	0.985	190.48
LFDM	0.128 ± 0.017	20.0 ± 1.23	35.6 ± 1.31	0.989	8.03

	Regression Parameter				
	Age	F	df	P	r^2
Lipid	0.39 ± 0.051	57.6	1,23	<0.0001	0.715

ymptotic LFDM mass rather than differences in the accumulation rate of LFDM (Fig. 1). The maximum accumulation rates of LFDM at the inflection point of the fitted curves were similar for the three species (0.97 g/day for Least Auklets, 1.10 g/day for South Georgia Diving Petrels, and 1.07 g/day for Common Diving Petrels). Predicted LFDM mass at fledging was 86.6% of adult LFDM for Least Auklets, 91.6% for adult LFDM for South Georgia Diving Petrels, and 84.4% of adult LFDM for Common Diving Petrels.

Fitted logistic equations had the lowest residual mean square for data on lipid accumulation in Least Auklets and South Georgia Diving Petrels (Table 3). The residual mean square for lipid content as a function of age in Common Diving Petrels was minimized by a linear model (Table 3, Fig. 2). The 95% confidence limits about the growth rate constants (K) of lipid accumulation in Least Auklets and South Georgia Diving Petrels overlapped considerably, and maximum rates of lipid accumulation at the inflection point were similar (1.0 and 1.1 g/day,
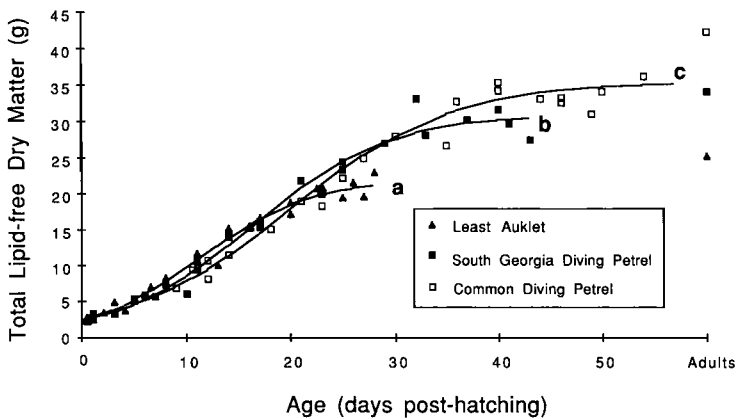

Fig. 1. Age-specific lipid-free dry matter mass for nestling Least Auklets (a), South Georgia Diving Petrels (b), and Common Diving Petrels (c). Curves represent logistic equations fitted to the data for each species. Values for adults are averages ($n = 6$) for each species.
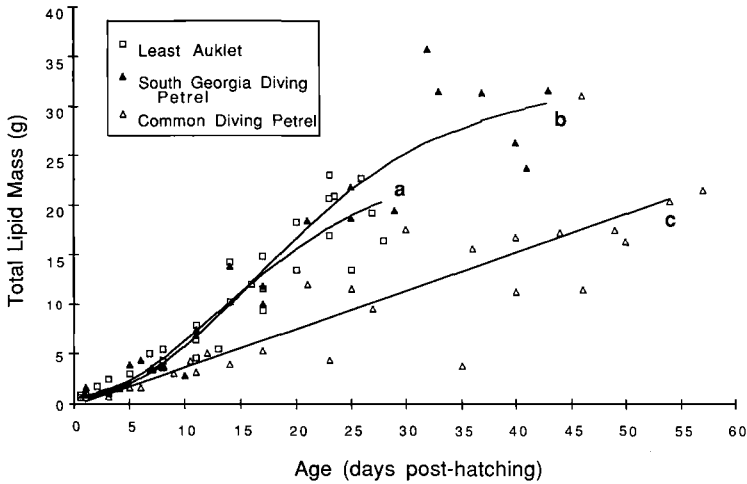
Fig. 2.   Age-specific lipid mass for nestling Least Auklets (a), South Georgia Diving Petrels (b), and Common Diving Petrels (c). Curves represent logistic equations fitted to the data from nestling Least Auklets and South Georgia Diving Petrels, and the least squares regression for data from nestling Common Diving Petrels.

respectively). The predicted lipid content of South Georgia Diving Petrels at fledging (30 g) was 50% higher than in Least Auklets (20 g). However, the ratio of lipid mass to LFDM mass in fledglings was similar in the two species (Least Auklet: 0.91, South Georgia Diving Petrel: 1.12). Common Diving Petrel chicks accumulated lipid at a significantly lower rate than the other two species (slope = 0.39 g/day, SE = 0.051) and, despite larger fledgling mass and a nesting period almost twice as long as that of Least Auklets, fledged with similar lipid stores (21 g). The ratio of lipid mass to LFDM mass in Common Diving Petrels at fledging was only 0.50. In all three species, average fledgling lipid reserves were considerably higher than those of adults; lipid content of adults during the chick-rearing period averaged 4.9 g for Least Auklets, 11.5 g for South Georgia Diving Petrels, and 8.7 g for Common Diving Petrels, only 25–41% that of their respective fledglings.

In the three species, residual mean square values indicated that measurements of accumulated lipid varied more about the fitted curves than measurements of accumulated LFDM (Table 3) (i.e. accumulation rates of LFDM varied within narrow limits). This supports the conclusion that lipid deposition was dependent on the level of surplus dietary energy once maintenance and LFDM accumulation requirements had been met.

Respired energy.—Estimates of respired ener-

gy were similar in the three study species during the first 5 days after hatch, when chicks of all species were brooded continuously (Fig. 3). After day 5 the curves diverged, primarily as a consequence of interspecific differences in length of the brooding period. At day 8 post-hatch, South Georgia Diving Petrel chicks were brooded for approximately 17% of the day, Least Auklet chicks for approximately 79%, and Common Diving Petrel chicks for the entire 24-h period. Estimated daily energy expenditure for diving petrel chicks increased sharply when continuous brooding ended. Unlike the diving petrels, the incidence of brooding in Least Auklets declined gradually and estimated daily energy expenditure did not increase sharply.

In all three species, daily respired energy increased during the first half of the nestling period and remained approximately constant thereafter (Fig. 3). Least Auklet chicks reached an asymptotic respiration rate at approximately 120 kJ/day, South Georgia Diving Petrel chicks at 155 kJ/day, and Common Diving Petrel chicks at 145 kJ/day.

Energy budgets of nestlings.—The energy equivalent of growth (lipid-free dry matter plus biosynthesis) for Least Auklets increased to a maximum of 27 kJ/day at day 11 post-hatch (18% of total energy budget) and then declined gradually until fledging. Growth declined from a maximum of 33% of total energy budget shortly after hatch to approximately 5% at fledging
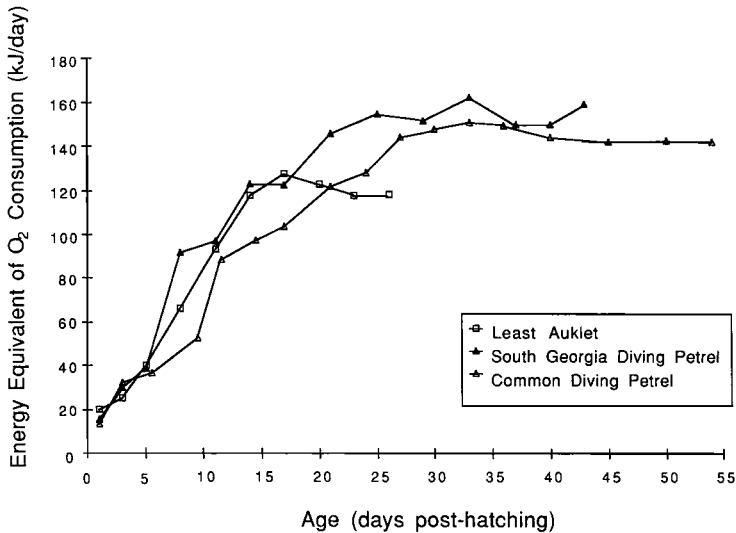
Fig. 3.   Age-specific daily respired energy for nestling Least Auklets, South Georgia Diving Petrels, and Common Diving Petrels, calculated from temperature-specific oxygen consumption rates and parental brooding schedules.

(Fig. 4a). In South Georgia Diving Petrels, energy equivalent of growth peaked at 31 kJ/day on day 14 (17% of total budget). As a proportion of total daily energy budget, growth declined from 35% shortly after hatching to about 1% at fledging (Fig. 4b). In Common Diving Petrels, the energy equivalent of growth peaked at 31 kJ/day on day 21 (19% of total budget). Growth declined from 29% of total energy budget at hatching to 1% at fledging (Fig. 4c).

The energy equivalent of lipid accumulation was twice the energy equivalent of growth during the latter half of the nestling period in Least Auklets and South Georgia Diving Petrels (Fig. 4: a, b). In contrast, the energy equivalent of lipid accumulation in Common Diving Petrel nestlings was less than that for growth during much of the nestling period (Fig. 4c).

Estimates of total daily energy requirements peaked at 176 kJ/day in Least Auklets, at 204 kJ/day in South Georgia Diving Petrels, and at 178 kJ/day in Common Diving Petrels. Despite the similarity in peak nestling mass of South Georgia Diving Petrels (142 g) and Common Diving Petrels (134 g), estimated maximum energy requirement was 15% higher in the former. The peak nestling mass for Least Auklets (91.5 g) was 32% less than for Common Diving Petrels, yet maximum energy requirements were virtually identical. The low relative energy requirement of Common Diving Petrels was pri-

marily due to lower rate of lipid deposition. Maximum energy requirement for fat deposition coincided with high energy requirements for maintenance and growth in Least Auklets and South Georgia Diving Petrels. The peak in total daily energy requirement was less pronounced in Common Diving Petrels, which deposited lipid at a constant rate throughout the nestling period (Fig. 4: a–c).

Estimated total energy intake of chicks was 193 kJ/day for Least Auklets, 246 kJ/day for South Georgia Diving Petrels, and 202 kJ/day for Common Diving Petrels (Table 4). Estimates of maximum energy requirements for the three species were 91%, 83%, and 88% of estimated total energy intake, respectively. Consequently, interspecific differences in estimated daily energy intake were matched by differences in estimated daily energy requirement. If parents of the three study species cannot increase the rate of energy delivery to the nest, then chick energy budgets are apparently constrained by average energy intake.

DISCUSSION

Diet composition.—Wax esters are a readily assimilable component of chick diets (Place and Roby 1986, Roby et al. 1986). Wax esters comprised 86% of lipids in the diet of Least Auklet chicks, equivalent to 115 kJ/day. This is more
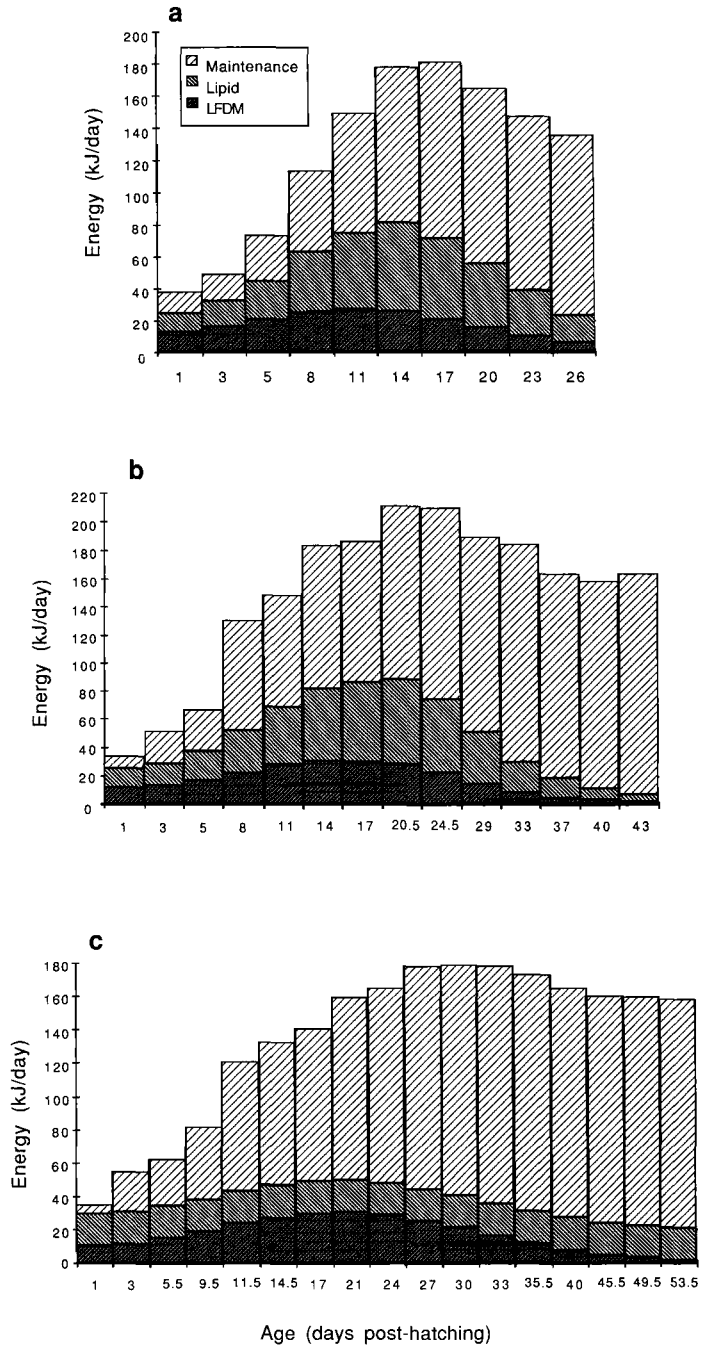
Fig. 4a–c. Age-specific daily energy budgets of Least Auklet (a), South Georgia Diving Petrel (b), and Common Diving Petrel (c) chicks calculated from rates of accumulation of lipid and lipid-free dry matter (LFDM) and daily respired energy. Values for energy equivalents of lipid and LFDM accumulation include the estimated energy cost of biosynthesis.

Table 4. Calculations for average daily energy intake of nestling Least Auklets, South Georgia Diving Petrels, and Common Diving Petrels. Means are ±SD.

	Least Auklet	South Georgia Diving Petrel	Common Diving Petrel
Lipid[a]			
Content (% of wet mass)	9.6 ± 1.75	8.7 ± 1.46	4.5 ± 1.43
Intake (g/day)	3.39 ± 1.52	3.71 ± 1.17	2.18 ± 0.89
Energy (kJ/day)	133.9 ± 60.04	146.5 ± 46.22	86.1 ± 35.16
Protein[b]			
Content (% of wet mass)	7.2 ± 0.66	10.7 ± 0.24	10.8 ± 0.22
Intake (g/day)	2.54 ± 1.06	4.56 ± 1.22	5.24 ± 1.34
Energy (kJ/day)	45.9 ± 19.08	82.3 ± 21.96	94.1 ± 24.12
Chitin and carbohydrate[c]			
Content (% of wet mass)	1.3	1.4	1.5
Intake (g/day)	0.47 ± 0.188	0.59 ± 0.160	0.74 ± 0.186
Energy (kJ/day)	8.1 ± 3.23	10.1 ± 2.75	12.7 ± 3.20
Total energy			
Intake (kJ/day)	193 ± 63.1	246 ± 51.25	202 ± 42.76

[a] Energy equivalent of lipid = 39.5 kJ/g.
[b] Energy equivalent of protein = 18.0 kJ/g.
[c] Estimated from published values; energy content of chitin and carbohydrate = 17.2 kJ/g.

than sufficient to meet the peak maintenance requirements of nestlings (112 kJ/day). Approximately 60% of the estimated energy content of chick meals was in the form of wax esters, and 65% of estimated assimilated energy was from wax esters. Adult Least Auklets specialize on calanoid copepods during the breeding season (Bédard 1969) and the high energy requirements of chicks are met by the high lipid content of calanoid copepods. The ability to metabolize wax esters is an essential adaptation for utilization of this food source.

Approximately 40% of dietary lipids for South Georgia Diving Petrels and 25% for Common Diving Petrels consisted of wax esters. This is equivalent to a daily intake of 59 kJ (29% of total energy intake) for South Georgia Diving Petrel chicks and 21 kJ (12%) for Common Diving Petrel chicks. Dietary wax esters supplied more than the energy equivalent of deposited lipid plus the energy costs of adipose tissue biosynthesis in both diving petrel species. Although less prevalent in diving petrel chick meals, wax esters nevertheless provide an important, highly assimilable source of energy for both taxa of seabirds.

The small size of calanoid copepods (4–8 mm) may limit their suitability as high-energy prey for all but the smallest planktivorous seabirds. Dovekies (Alle alle), the smallest North Atlantic alcid, specialize on calanoid copepods (Norder-

haug 1980, Evans 1981, Roby et al. 1981). Like Least Auklets, Dovekie chicks deposit large fat reserves (21 g) before fledging (Taylor and Konarzewski 1989). Parakeet Auklets (Cyclorrhynchus psittacula) and Crested Auklets (Aethia cristatella) are large planktivorous auklets (250–300 g), and their diet consists of approximately 20% and 10% of the larger calanoid copepods, respectively (Bédard 1969). In the Southern Ocean, Euphausia superba replaces calanoid copepods as the dominant grazing zooplankter, and no small planktivorous seabirds are known to specialize on calanoid copepods.

The lipid content of Least Auklet meals (9.6% of wet mass) is high compared with other plankton diets. However, the lipid content of calanoid copepods is exceeded by other nonplanktonic seabird prey (e.g. herring, Clupea harengus, is 13.6% lipid, and mackerel, Scomber scombrus, is 18.6% lipid; Montevecchi et al. 1984). The lipid content (4%) and energy density (3.89 kJ/g) of krill (Clarke 1980) is similar to that of capelin (Mallotus villosus; 3.3% lipid and 3.99 kJ/g energy density), an important food source for piscivorous seabirds breeding in the North Atlantic region (Montevecchi and Piatt 1984, Montevecchi et al. 1984). Thus the lipid contents and energy densities of high latitude planktonic crustacea fall within the range of values reported for important fish prey of seabirds.

Protein content was only 7.2% of wet mass in auklet meals, compared with 10.7% in diving petrel meals. The protein index (100 × g protein/kJ) for auklet chick meals was 1.3, compared with 1.9 in South Georgia Diving Petrel meals, and 2.6 in Common Diving Petrel meals. Protein content for a variety of nonplankton seabird prey (fish and squid) ranges from 14–20% of wet mass, higher than either the auklet or diving petrel meals, and protein indices range from 1.4–3.7 (Clarke and Prince 1980, Montevecchi et al. 1984). The low protein content and high lipid content of high latitude calanoid copepods raises the possibility of a dietary protein deficiency for growing Least Auklets. Nevertheless, the growth rate of Least Auklet chicks at the inflection point was 1.0 g LFDM/day, much less than the estimated 2.55 g of crude protein that chicks ingested on a daily basis. (Williams et al. [1977] estimated that LFDM was 94% protein in penguins.) Whereas estimates of crude protein from measurements of total nitrogen may overestimate actual protein content (Clarke 1980), the assimilation efficiency for dietary protein is probably close to 95% (Robbins 1983). This indicates a dietary surplus of protein and suggests that more than half of assimilated protein was metabolized by Least Auklet chicks as an energy source. Also, Least Auklet chicks grew at a similar rate compared with the diving petrel chicks despite higher protein levels in the diets of the latter (Table 3). I believe that dietary protein does not limit growth in the three study species.

Diet and chick lipid reserves.—I have shown, by carcass analysis, that Least Auklets and South Georgia Diving Petrels deposited lipid at similar rates and fledged with similar lipid reserves relative to LFDM mass. However, Common Diving Petrel nestlings accumulated lipid at a lower rate than either of the other study species and, despite a longer nestling period, fledged with lower lipid reserves.

Lipid deposition rates are presumably determined by the daily surplus of assimilated energy, once maintenance and growth requirements have been met. Consequently, interspecific differences in lipid deposition rate were a function of interspecific differences in energy intake, maintenance requirements, growth requirements, or some combination of these factors. I have shown that the higher lipid deposition rates of Least Auklets and South Georgia Diving Petrels were not a function of

lower energy requirements for either maintenance or growth. Instead, lipid deposition was enhanced by the high lipid content of the diet. The diet of Common Diving Petrels was dominated by *E. superba* and had a lower lipid content and a lower energy density than the diets of the other study species. The energy supplied by dietary lipids in Least Auklets (134 kJ/day) and in South Georgia Diving Petrels (147 kJ/day) was sufficient to meet the maximum combined energy requirements for both maintenance and biosynthesis (128 kJ/day in Least Auklets and 146 kJ/day in South Georgia Diving Petrels). Presumably, once growth requirements for protein had been met, any additional assimilated protein was metabolized to meet maintenance costs, and the energy saved was stored as fat. In Common Diving Petrels, the energy supplied by dietary lipids (86 kJ/day) was only 57% of the respired energy (maintenance and biosynthesis). The difference (65 kJ/day) must have been supplied by catabolizing other diet components, primarily protein. The important conclusion is that, even if Common Diving Petrel chicks assimilated all the available energy in the form of lipid, carbohydrate, and chitin, approximately half of the dietary protein must have been metabolized to meet energy requirements for maintenance and biosynthesis.

The nestlings of all three species accumulated substantial lipid reserves by fledging age. Both Least Auklets and South Georgia Diving Petrels had sufficient energy reserves at fledging to survive in the nest ca. 1 week without food. Common Diving Petrels could have survived ca. 5–6 days without food. Lack (1968) and O'Connor (1978) suggested that nestling lipid reserves are adjusted to variation in feeding frequency and that the large fat depots of seabird chicks insure survival during periods when adults fail to deliver food. The energy reserves of the three species I studied were far in excess of those required for chicks normally fed on a daily basis. The large fat depots of Least Auklets relative to Common Diving Petrels were particularly unexpected, given the high frequency of feeding in Least Auklets. Similarly, Leach's Storm-Petrel chicks accumulate large fat depots (up to 30 g) sufficient to meet maintenance requirements for >2 weeks (Ricklefs et al. 1980a), but intervals between feedings rarely exceed 3 days (Ricklefs et al. 1985). Instead, the characteristic large fledging fat reserves of many sea-

birds may be an adaptation to enhance post-fledging survival.

Both auklets and diving petrels receive no postfledging parental care, and large energy reserves may be important for postfledging survival. No data are available on the relationship of fledgling fat reserves to postfledging survival, but some studies indicate that fledgling mass is positively correlated with postfledging survival (Perrins 1966, Perrins et al. 1973, Jarvis 1974). The large prefledging fat stores of other seabirds that receive no postfledging parental feeding suggest that energy reserves play an important role in postfledging survival (Burger 1980, Ricklefs et al. 1980a, Montevecchi et al. 1984). In seabirds with extended periods of postfledging parental care, lipid reserves at fledging are substantially smaller (Burger 1980, Shea 1985).

Diet and brooding period.—A major problem in the rearing of pelagic seabird chicks is the transition to thermal independence, particularly in species that breed in cold climates. The chick-brooding period imposes maximum demands on food acquisition by adults, which must obtain sufficient food for (1) the round-trip between feeding area and nest site, (2) maintenance and chick-brooding during the brooding shift, and (3) the growing chick (Ricklefs 1983). This implies that adults should seek to terminate brooding as early as possible. The transition to thermal independence is particularly abrupt for the young of seabirds that visit the nest site only at night, such as diving petrels. During the day, a parent can either remain in the nest and brood its chick, thus limiting to one the number of meals delivered, or it can feed at sea and leave the nestling unattended for the entire day. South Georgia Diving Petrel chicks were brooded continuously until 6–7 days old and Common Diving Petrel chicks until 11–12 days old, which matched closely the respective periods required for development of homeothermy (Ricklefs and Roby 1983).

Chicks must store sufficient energy reserves to support maintenance costs between feedings before they can be left unattended in the nest. These energy reserves can be expressed as estimated survival time (i.e. the period that stored lipids could provide maintenance requirements in the absence of brooding). During the first week post-hatch, South Georgia Diving Petrels accumulated lipid reserves at a rate ca. 0.55 g/day compared with 0.39 g/day in Common Diving

Petrels (Fig. 2). By the end of the brooding period (7 days), South Georgia Diving Petrels had accumulated sufficient fat reserves to survive for more than a day without food. Common Diving Petrels did not accumulate comparable energy reserves until approximately 11 days post-hatch, when brooding ceased in this species. The length of the brooding period apparently matches the time required for the chick to accumulate sufficient energy reserves to survive the period between meals without a parent in attendance. The longer brooding period of Common Diving Petrels was necessitated by the lower energy intake rates of chicks, which in turn was a function of the lower lipid content of the diet.

Dietary energy and growth.—Ricklefs (1979, 1984) has shown that most of the variation in avian growth rate can be explained by differences in adult body mass. Much of the residual variation in growth rate is a function of mode of development, with young that are altricial at hatch growing at a higher rate than precocial young. The three study species share a semi-precocial mode of development. They are down-covered at hatch, are capable of maintaining body temperature at an early age, and remain in the nest until fully grown. Consequently, once growth rate is adjusted for differences in adult body mass, differences in growth rate among the study species would be expected to be largely a function of dietary differences. While the higher lipid content of Least Auklet and South Georgia Diving Petrel chick meals was responsible for higher lipid deposition rates compared with Common Diving Petrels, growth rate (accumulation of LFDM) was not significantly higher. This indicates that differences in energy intake were not reflected in differences in the nonlipid components of growth.

Nevertheless, the low energy content of Common Diving Petrel chick meals may prolong the nestling period by failing to supply a sufficient daily surplus of energy to meet minimal lipid deposition rates. A large proportion of dietary protein must be metabolized by Common Diving Petrel chicks to meet maintenance energy requirements, because of the low lipid content of the diet. Common Diving Petrels fledge at a lower percentage of adult mass compared with South Georgia Diving Petrels and little additional growth occurs during the last 10 days of the nestling period (Figs. 1 and 4c). On the other hand, lipid deposition rate is ap-

proximately constant throughout the nestling period (Fig. 2), and a major advantage to the longer nestling period of Common Diving Petrels may be the additional accumulation of fat reserves prior to fledging.

Postnatal development in auklets and diving petrels may not be energy-limited if adults can provide additional food for their chicks. Twinning experiments (Nelson 1964, Harris 1970) and cross-fostering experiments (Shea and Ricklefs 1985) indicate that some seabirds respond to increased nestling demand with increased food delivery rates. However, there are indications that the three study species feed their chicks at close to the maximum rate. Twinning experiments with alcid species have invariably resulted in failure to successfully raise both young to normal fledging mass (reviewed in Gaston 1985). Also, the considerable intercolony variation in growth rates and fledgling mass in some alcid species (reviewed in Gaston 1985) suggests that food supply is frequently insufficient to support maximal growth. For nocturnal seabirds, like diving petrels, it is probably impossible for adults to deliver more than one chick meal each night. Compared with other procellariiforms, diving petrel chick meals are larger (Roby 1989) and wing loadings higher (Warham 1977a). This suggests that meal volume is constrained. Finally, the adults of the three study species exhibit relatively high free-ranging metabolic rates during the chick-rearing period (Roby and Ricklefs 1986). This indicates that parents forage at close to a maximum rate. Consequently, planktivorous seabirds that forage farther offshore and cannot feed their young each night must either provide meals with a higher energy density or reduce energy requirements at the nest.

Auklets and diving petrels feed their young essentially fresh food, and parents do not enhance the lipid content of chick meals by selectively assimilating or excreting nonlipid dietary components. However, all procellariiform seabirds other than diving petrels form stomach oils in the proventriculus during foraging bouts at sea, and they feed their young a diet with a higher energy content than fresh food (Warham 1977b). The formation of stomach oils allows parent seabirds to consume foods, such as the abundant *E. superba*, with a low lipid-to-protein ratio relative to the requirements of their young (Obst 1986). Chick meals that contain stomach oils potentially avoid energy constraints on postnatal development. This results in (1) earlier cessation of brooding due to higher rates of lipid deposition in neonates and the consequent freeing of adults to forage full-time, (2) shorter nestling periods due to sufficient dietary lipid to meet maintenance and biosynthesis requirements, and (3) larger chick lipid reserves at fledging.

The postnatal development of Antarctic Prions (*Pachyptila desolata*) and Blue Petrels (*Halobaena caerulea*) supports the hypothesis that supplementation of plankton diets with stomach oils results in shorter nestling periods. Antarctic Prions feed their young mostly *E. superba,* but chick meals include on average 20% stomach oils (Prince 1980b). The chicks are brooded for only 0–5 days post-hatch (Tickell 1962) and meet the energy demands of homeothermy by metabolizing stomach oils supplied by the parents (Simons and Whittow 1984). Despite larger adult mass (160 g), Antarctic Prions have a shorter average nestling period (50 days; Tickell 1962) than Common Diving Petrels. Nestlings deposit lipid at higher rates (1.5 g lipid/day; D. D. Roby unpubl. data) than do diving petrel chicks, and fledging mass averages 13% higher than adult mass (Tickell 1962), which indicates that chicks fledge with considerable fat reserves. Blue Petrels are larger than Antarctic Prions (average adult mass: 193 g), yet the nestling period is shorter and chicks fledge at a larger mass relative to adults. Blue Petrel chick meals consist of approximately equal proportions of *E. superba* and fish, but the proportion of stomach oils in chick meals is higher than in Antarctic Prions (39% of wet mass on average; Prince 1980b).

However, many procellariiform seabirds that feed their chicks stomach oils do not exhibit high growth rates and short nestling periods. For example, Leach's Storm-Petrels are smaller than the species in this study (45 g), but growth rates are considerably lower (maximum accumulation rate of LFDM = 0.25 g/day) and nestling periods are longer (65–70 days; Ricklefs et al. 1980b). Nestlings deposit up to 35 g of fat, a portion of which must be metabolized before going to sea (Ricklefs et al. 1980a). Postnatal development in Leach's Storm-Petrel is clearly not energy-limited. Instead, tissue-level constraints apparently limit growth to levels far below what energy intake will permit. Additional experimental work on slow-growing seabirds is needed in order to elucidate the relative

contribution of diet and tissue constraints for limiting growth.

My study supports the hypothesis that patterns of postnatal development in seabirds are related to diet. Differences in diet composition, specifically lipid content, among the study species were associated with differences in chick energy budgets and development. Energy budgets indicated that maintenance energy requirements of chicks were high relative to energy provided by the parents. Parents were apparently providing food to their nestlings at or near the maximum rate.

Calanoid copepods, which formed the bulk of the Least Auklet diet, contained considerable quantities of wax esters, which provided most of the energy requirements of chicks. The diet of Common Diving Petrel chicks was relatively low in dietary lipid and considerable dietary protein was metabolized in order to meet maintenance energy requirements. The study species lack postfledging parental care; large lipid reserves at fledging presumably enhance postfledging survival.

While differences in diet composition were sufficient to explain much of the interspecific variation in chick development in these seabirds, there was no significant interspecific difference in accumulation rate of LFDM. This supports the conclusion that growth (accumulation of LFDM) is not constrained by energy intake. High lipid diets were associated with higher rates of lipid deposition by chicks, but not higher growth rates. Instead, constraints operating at the level of tissues are apparently responsible for most of the variation in growth rate among seabirds.

The formation of stomach oils enables breeding procellariiform seabirds (except diving petrels) to enhance the lipid content of the diet and supply the high energy requirements of their young. However, many seabirds that feed their young stomach oils have lower growth rates and longer nestling periods, indicating that postnatal development is frequently not energy-limited. Twinning and cross-fostering experiments also indicate that some seabirds are capable of increasing the rate of energy delivery to the nest, suggesting that not all seabirds are foraging at the maximum rate when feeding young. Apparently, tissue-level constraints are the primary factor limiting growth rate in many seabird species, while others may experience energy intake constraints that militate maximal

growth. Further studies of feeding rates and diet composition in relation to chick energy budgets will enhance our understanding of the ecological factors that shape observed patterns in seabird reproduction.

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