

# STOMACH OIL AND THE ENERGY BUDGET OF WILSON'S STORM-PETREL NESTLINGS<sup>1</sup>

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**Abstract.** Aspects of chick-provisioning in Wilson's Storm-Petrel were measured at Palmer Station, Antarctica. Chicks received meals averaging 9.2 g (21% of adult body mass) with a mean frequency of 1.1 feeds/chick·day. Feeding frequency decreased as chicks grew, but meal mass remained relatively constant throughout the fledging period. Free lipids accounted for an average of 24% of the mass and over 60% of the energy in a meal. The energy density of the meals averaged 16.1 kJ/g, nearly triple that of whole prey. The estimated rates at which gross and metabolizable energy were delivered to the chick averaged 163 and 147 kJ/days, respectively, over the 60 day fledging period.

Low nest temperatures resulted in high energy requirements by the chicks. Rates of respiratory energy metabolism averaged 133 kJ/day over the fledging period and reached peak levels of ~160 kJ/day. Rates of energy deposition in tissues averaged only 18.4 kJ/day with a peak rate of ~57 kJ/day. Thus, total metabolizable energy requirements of the chick averaged 151 kJ/day, which is within 3% of estimated metabolizable energy intake.

Wilson's Storm-Petrel chicks have energy requirements nearly double those of Leach's Storm-Petrel chicks which grow in a more temperate climate. Wilson's Storm-Petrel adults appear to meet demands of their chicks with a high frequency of meal delivery and high energy density of meals compared to those of Leach's Storm-Petrel. A comparison of the rates of energy utilization by foraging adults of the two species suggests that the high energy demands of the Wilson's Storm-Petrel chicks have selected for a foraging strategy in adult Wilson's Storm-Petrels that is expensive in terms of energy and time.

Low air temperatures, a short summer season, and the presence of diurnal predators on the breeding grounds are among the factors which have shaped the chick-provisioning strategy of this species. The data suggest that Wilson's Storm-Petrels could not breed successfully in the Antarctic without the ability to produce stomach oils.

*Key words:* Body composition; diet; feeding behavior; food provisioning; foraging strategy; growth energetics; growth rate; meal composition; metabolic rate.

## INTRODUCTION

The problems that pelagic seabirds face in provisioning their young have been a central issue in seabird ecology (Ashmole 1963a, 1963b; Lack 1966, 1968; Ricklefs 1983; Pennycuik et al. 1984; Montevecchi et al. 1992). The presumed difficulties that adult seabirds have in acquiring and transporting energy for their chicks have been repeatedly offered as an explanation for the convergent evolution of a suite of life-history characteristics (small clutch size, long incubation period, slow growth, delayed reproduction, and long life span) common to pelagic seabirds belonging to several taxonomic orders. Yet, surprisingly few studies have included measurements of all the relevant parameters that comprise provisioning of the chicks of a given species.

Among marine birds, procellariiforms are unique in their ability to produce "stomach oil," which was originally defined as the oily fluid found in the proventriculus. Stomach oil is part of the meal given to the chicks by their parents. Considerable attention has been given to the composition, origin and function of stomach oil (Clarke and Prince 1976, 1980). This liquid contains much water but a substantial portion is free lipid (mainly neutral lipids), and it may also contain fat-soluble pigments and other dissolved organic substances (Ashmole 1971, Place et al. 1989). The free lipids come from the diet, becoming concentrated, rather than being produced in the proventriculus (Roby et al. 1986, 1989; Place et al. 1989). The function of stomach oils has been debated (see reviews by Warham et al. 1976 and Jacob 1982), but recent studies indicate a clear role in providing energy-rich meals to chicks (Simons and Whittow 1984, Roby et al. 1986, Ricklefs et al. 1987, Bech et al. 1988).

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Wilson's Storm-Petrel (*Oceanites oceanicus*), Antarctica's smallest endotherm, breeds abundantly at ambient temperatures near 0°C. Parents feed their single chick irregularly and only at night, and parental regurgitations include stomach oil (Roberts 1940, Beck and Brown 1972, Wasilewski 1986, Croxall et al. 1988). The species' small size, the low temperatures of the breeding habitat, and the nestling's early thermal independence (Roberts 1940) suggest that Wilson's Storm-Petrel chicks may have unusually high energy requirements, and that stomach oils may therefore play an important role in meeting chick energy demands. To test this hypothesis, we measured: (1) the frequency, mass, and energy content of meals delivered by the parents; (2) the quantity of stomach oil included in the meals; and (3) the energy expenditure of chicks of this species.

#### METHODS

*Mass and frequency of meals.* Field work was conducted on Bonaparte Point, 300 m from Palmer Station, in March 1984 and March 1986. Fifteen nests were studied in a colony of 100–150 pairs. Wilson's Storm-Petrels feed their chicks almost exclusively at night. At dusk, prior to the arrival of adults, each chick was removed from its nest crevice and weighed it to the nearest 0.5 g using a Pesola spring balance calibrated against Ohaus standards. Each chick was then returned to its nest, and was subsequently reweighed at 2–3 hr intervals through the night. An increase in mass between weighings signaled that a feed had occurred. Chicks were weighed at roughly 6 hr intervals between dawn and the following dusk to verify that no daytime feeds occurred.

Because weights were taken only every 2–3 hr, it was usually not possible to determine directly whether a mass increase resulted from feeding by one or by both parents. Furthermore, because some fraction of the body mass increase may have been lost to defecation and respiration by the chick, the mass increase recorded between weighings underestimated true meal size. Therefore, the size of the meals and the true frequency with which parents deliver meals were estimated from the mass increase data using methods described in detail by Ricklefs (1984) and Ricklefs et al. (1985).

According to these methods, the recorded mass increases were corrected for mass lost between

feeds by adding the mean amount of mass lost by individuals that were not fed during the period between weighings. The total mass fed to a chick per night was calculated as the sum of all such positive mass increases. Chicks were considered as having received no feed if their mass change between weighing was less than or equal to zero.

Double feeds were usually detectable as separate mass gain events in one night, but single instances of body mass increase that were clearly double the typical amount were also scored as double feeds. The proportions of the mass increases representing single (one parent) and double (two parent) feeds were estimated from the proportion of chicks receiving no feeds,  $Q^2$ , where  $(1 - Q)^2$  is the proportion of double feeds and  $1 - [Q^2 + (1 - Q)^2]$  is the proportion of single feeds.  $Q$  represents the probability that a given parent will not feed its chick on a given night, while  $1 - Q = P$  represents the probability that it will feed its chick.  $P$  also represents the mean feeding frequency of each parent (feeds/parent·night) and  $2P$  equals the feeding frequency for the chick (feeds/chick·night).

*Stomach oil in meals.* The mass of stomach oil, and the mass of the free lipid in the stomach oil were measured for 23 meals collected over three nights. Stomach oil was pumped from the stomachs of recently fed chicks. At dusk, prior to the arrival of adults, each chick was removed from its nest and its liquid stomach contents were drawn into a 5 ml syringe through a length of Tygon tubing inserted past the glottis and into the stomach. Narrow-diameter tubing was used so as to remove the liquid portion of the meal, and exclude most of the stomach solids from the sample. The last 2 cm of each tube was perforated with a series of small holes which improved liquid flow into the syringe. The stomach was pumped repeatedly until no additional liquid appeared in the tube. Then, each chick was weighed as described above and returned to its nest. When subsequent weighings signaled that a chick had been fed, its liquid stomach contents were again withdrawn using the syringe and tube apparatus. Each chick was reweighed and returned to its nest. Chicks were weighed throughout the night, but stomach contents were taken only after the first recorded mass increase for any given chick.

The stomach oil was transferred to a tared, screw-capped vial, kept cold in packed snow until the end of the night, and transported to Palmer Station for further processing. There, samples

were weighed to the nearest 0.1 g and warmed to room temperature to melt the free lipids in the stomach oil. The samples were centrifuged for 5 min to separate the liquid into a lipid and an aqueous layer. Any solid, flocculent material that entered the tube with the sample moved to the bottom of the vial with the aqueous layer. Solid matter comprised little of the volume of most stomach oil samples. The upper, lipid layer was carefully transferred by pipette to a second, tared vial and weighed to the nearest 0.1 g. The mass of the solid portion of each feed was calculated by difference between the total feed mass (from body mass increase) and the measured mass of the stomach oil.

The effectiveness of the stomach pumping technique at removing liquids from the stomach was tested in two ways. First, the stomachs of 10 adult Wilson's Storm-Petrels were pumped before sacrificing them and dissecting their stomachs. In no case could a substantial amount of additional stomach oil be retrieved by dissection of these stomach-pumped birds. Second, the stomachs of five chicks were emptied by pumping out the contents and holding them without feeding for three days. They were force fed 3 g of vegetable oil using a syringe and tube like the apparatus used to take stomach samples. Five minutes later, their stomachs were pumped in the usual manner and weighed the sample. The stomach pumping reclaimed ~85% ( $84.7 \pm 1.4\%$ ) of the vegetable oil. No additional oil was reclaimed by subsequent dissection, and the remainder most likely adhered to tissues of the crop and proventriculus. These tests suggest that although stomach pumping tends to underestimate the quantity of stomach oil in the stomach, it is no less effective than methods requiring that the chick be killed.

*Energy density of feeds.* The energy contents of nine free lipid samples taken from the centrifuged stomach oils were determined by the direct combustion of small, preweighed drops of the lipid in a Phillipson microbomb calorimeter calibrated with benzoic acid. Solid stomach contents remaining after the stomach oil had been removed by pumping were obtained by dissecting nine freshly fed chicks. The solids were homogenized with a mortar and pestle, formed into pellets, and dried. Pellets were weighed before and after drying to determine water content of the solids, and energy contents of the solids were then determined by microbomb calorimetry.

Finally, energy contents of five whole regurgitations from adults captured at the nest were determined by drying the homogenized regurgitations, forming pellets from aliquots of the homogenate, and doing microbomb calorimetry on the pellets. For each sample, two or three replicates were bombed, and the energy content of the sample was taken to be the mean of the replicate values. This allowed calculation of the energy content of the aqueous portion of stomach oil as the difference between energy contained in total stomach contents and that in lipid plus solid fractions.

*Energy requirements of the chicks.* The energy required by the chick for growth and maintenance was estimated as the sum of (1) the energy deposited in tissues, and (2) the energy used in respiration (energy metabolism by the chick).

Fourteen chicks ranging from 3–58 days of age were taken from the nest and sacrificed. Their stomach contents were removed by dissection and each carcass was weighed to the nearest 0.1 g. The carcasses were dried to constant mass at 60°C, and their water contents were determined from the difference in fresh and dry mass. The dried carcasses were chopped and the pieces were placed into individual paper, drip-coffee filter bags (Melita 16F). The bags were then stitched closed and weighed along with their contents to the nearest 0.1 g. Next, the bags were immersed in two one-gallon containers of petroleum ether for one week to extract lipids from the carcasses. The petroleum ether was circulated through the filter bags by constant stirring with a magnetic stir bar. The bags were then immersed in two one-gallon containers of stirred chloroform for a second week to extract any remaining lipids. Finally, the filter bags and their contents were rinsed in fresh chloroform, dried at 50°C, and reweighed. Lipid contents of the carcasses were determined from the difference in the masses of the filter bags before and after the extraction process. The lean dry mass (LDM) in each carcass was determined by subtracting the sum of its water and lipid masses from its fresh mass. The carcass energy contents were calculated assuming an energy equivalency of 38 kJ/g lipid and 20 kJ/g LDM.

Rates of energy metabolism were determined by measuring rates of oxygen consumption ( $V_{O_2}$ ) in chicks ranging between 2 and 60 days of age. Chicks were transported from Bonaparte Point to the laboratory at Palmer Station during the

day, when adults were out foraging, and were returned to the nest before sunset. (Measuring  $\dot{V}O_2$  only during daylight hours precluded detection of a possible circadian rhythm in chick energy metabolism, which would cause error in extrapolations of hourly to daily  $\dot{V}O_2$ ). Each chick was weighed and placed in a dark, black-walled, steel chamber. The temperature of the chamber was maintained between 1 and 3°C (the range of the mean nest temperatures measured at five nests on Bonaparte Point; see below) by immersing it in a Haake N-3 waterbath. Outside air was pumped through a column of ascarite and drierite to remove  $CO_2$  and  $H_2O$  respectively. The flow rate of dried air into the chamber was regulated with a rotometer such that the chick's oxygen consumption never reduced the  $O_2$  content of the chamber air to below 20% (i.e., flow rates between 400 and 800  $cm^3/min$ ). Air leaving the chamber was passed through a second ascarite/drierite column before reaching a Beckman E-2 paramagnetic oxygen analyzer. Set on the 20–21% range, the analyzer measured the  $O_2$  content of the air to 0.001%. Gas volumes were corrected to units of standard temperature and pressure, and  $\dot{V}O_2$  was calculated using equation 2 of Hill (1972).  $\dot{V}O_2$  was converted to units of energy consumption assuming an equivalency of 20.1 J/ $cm^3O_2$  consumed. This equivalency varies with diet composition, and may introduce 1–2% errors in estimated rates of heat production.

*Age determination of chicks.* Because the study was begun after most of the chicks had hatched, the exact age of most chicks was not known. The ages of these chicks were estimated using mensural and plumage criteria given in Beck and Brown (1972) and Roberts (1940). These criteria include lengths of tarsus, wing, culmen, tail, and outer primaries, the color of soft parts, and the pattern of down. Testing these criteria on birds of known age, we found that age estimates were accurate to within about  $\pm 3$  days, or 5% of the total fledging period.

*Nest temperatures.* Temperatures inside five nest crevices were determined using thermistors connected to a Campbell Scientific data logger, model CR21. Thermistors were suspended in the nest chambers within 25 cm of the resident chick, and an additional thermistor measured shaded air temperature. The data logger sampled air temperature from the output of these 6 thermistors once each minute throughout the day for four weeks (March 2–29, 1986). Mean, maxi-

TABLE 1. Proportions of Wilson's Storm-Petrel nestlings fed and not fed during seven nights at Palmer Station, Antarctica.

Date	Number of chicks fed (%)	Number of chicks not fed (%)	Total	$P^a$
7 Mar 1984	6 (85.7)	1 (14.3)	7	0.622
8 Mar 1984	7 (53.8)	6 (46.2)	13	0.321
9 Mar 1984	13 (92.9)	1 (7.1)	14	0.733
16 Mar 1984	9 (81.8)	2 (18.2)	11	0.574
22 Mar 1984	9 (81.8)	2 (18.2)	11	0.574
14 Mar 1986	9 (81.8)	2 (18.2)	11	0.574
20 Mar 1986	10 (83.3)	2 (16.7)	12	0.592
Combined	63 (79.7)	16 (20.3)	79	0.550
SE	(4.6)	(4.6)		0.047

<sup>a</sup>  $P$  is the probability that an individual parent feed its chicks on a given night. The method for calculating these probabilities is described in the text.

imum, and minimum nest temperatures were recorded for each 30-min and each 24-hr period.

## RESULTS

*Feed mass and frequency.* No mass increase was recorded on 16 (20.3%) of 79 chick nights (Table 1). The percentage of chicks not receiving feeds on any single night ranged from 14.3 to 46.2%, but these percentages were not statistically different from one another ( $\chi^2 = 7.23$ ,  $df = 6$ ,  $P = 0.30$ ). After pooling the data from all seven nights (with a combined  $Q^2 = 0.203$ ), the calculated probability that a given parent feeds its chick on a particular night was  $P = 1 - (0.203)^{1/7} = 0.550$  (95% confidence interval = 0.436 to 0.664), and the average feeding frequency was  $2P = 1.10$  meals/chick·night. No daytime feeds were recorded during this study.

The mean rate of mass loss ( $\pm SE$ ) between night-time weighings for those chicks that were not fed was  $-0.64 \pm 0.10$  g/hr ( $n = 81$ ). There were no significant differences ( $P > 0.05$  via  $t$ -tests) among rates of mass loss during weighings intervals just prior to the first feed ( $0.70 \pm 0.23$  g/hr;  $n = 22$ ), intervals immediately following a feed ( $0.61 \pm 0.12$  g/hr;  $n = 37$ ), and later, post-feed intervals ( $0.62 \pm 0.17$  g/hr;  $n = 22$ ).

Summed nightly mass increases (adjusted for rates of mass loss between weighings) ranged between 0 and 23.3 g/chick. The mean of these nightly sums (including the 16 individuals for which no mass increase was recorded) was  $10.30 \pm 0.21$  g. The estimated proportion of these increases representing double feeds is 0.303, or approximately 17 out of the 56 chick nights. As-

TABLE 2. Stomach oil delivered to Wilson's Storm-Petrel chicks. Values are grams or percent.

Date	Nest	Body mass increment	Estimated feed mass	Stomach oil		Free lipid		Solids		
				Mass	%	Mass	%	Mass	%	
9 Mar	1	8.0	9.3	2.1	22.6	0.6	6.5	7.2	77.4	
	4	16.0	17.3	3.5	20.2	1.7	9.8	13.8	79.8	
	5	13.5	14.8	8.5	57.4	5.9	39.9	6.3	42.6	
	8	19.0	20.3	9.1	44.8	6.4	45.7	11.2	55.2	
	12	11.5	12.8	10.6	82.8	7.0	54.7	2.2	17.2	
	$\bar{x}$	14.13	15.40	6.76	45.6	4.32	45.7	11.2	55.2	
	SE	2.03	2.08	1.67	11.6	1.32	54.7	2.2	17.2	
16 Mar	1	13.0	14.7	3.3	22.4	0.6	31.3	8.14	54.4	
	2	2.5	4.2	1.3	30.9	0.3	9.8	2.01	11.6	
	3	20.0	21.7	8.1	37.3	5.6	4.1	11.4	7.6	
	4	14.0	15.7	6.0	38.2	3.4	7.1	2.9	69.0	
	6	14.0	15.7	5.3	33.8	3.2	25.8	13.6	62.7	
	8	8.0	9.7	5.6	57.7	3.8	21.7	9.7	61.8	
	10	4.0	5.7	1.1	19.3	0.4	20.4	10.4	66.2	
	11	10.0	12.3	4.2	34.1	1.7	39.2	4.1	42.3	
	15	7.5	9.2	5.6	60.9	3.7	7.0	4.6	80.7	
	$\bar{x}$	10.33	12.10	4.50	37.2	2.52	13.8	8.1	65.9	
	SE	1.84	1.84	0.76	4.7	0.62	40.2	3.6	39.1	
22 Mar	1	5.0	7.3	1.2	16.4	0.6	19.9	7.60	62.8	
	2	8.0	10.3	3.5	34.0	0.4	4.5	1.30	4.7	
	3	10.5	12.8	6.3	49.2	3.3	8.2	6.1	83.6	
	4	9.0	11.3	2.6	23.0	0.8	3.9	6.8	66.0	
	5	5.0	7.3	1.6	21.9	0.6	25.8	6.5	50.8	
	6	8.0	10.0	2.9	28.2	1.5	7.1	8.7	77.0	
	11	9.0	11.3	2.5	22.1	1.9	14.6	7.4	71.8	
	12	5.5	7.8	3.4	43.6	2.8	16.8	8.8	77.9	
	13	10.5	12.8	3.0	23.4	1.9	35.9	4.4	56.4	
	$\bar{x}$	7.83	10.13	3.00	29.1	1.53	14.8	9.8	76.6	
		SE	0.73	0.73	0.48	3.7	0.34	15.0	7.13	70.9
	Total	$\bar{x}$	10.06	11.94	4.41	35.8	2.45	20.5	7.53	64.2
		SE	0.93	0.93	0.54	3.4	0.42	3.1	0.66	3.4

suming that the largest mass increases can be attributed to double feeds, these 17 values ranged between 13.8 and 23.3 g, and averaged  $17.15 \pm 1.35$  g. The remaining 27 mass increases, representing single feeds, ranged from 4.2 to 12.8 g, with a mean of  $9.18 \pm 0.95$  g.

In six cases, chicks were known to have been fed twice on a given night because two separate increases were recorded. These 12 individual mass increases were thus known to represent single feeds. They ranged from 4.8 to 13.7 g and averaged  $8.81 \pm 1.98$  g, very similar to the range and mean of the presumed single feeds calculated above. Furthermore, the sums of these 6 pairs of mass increases ranged from 14.4 to 23.3 g with a mean of  $17.62 \pm 3.21$  g, very similar to the corresponding values for the presumed double feeds.

*Stomach oil in meals.* Total amounts of liquid

(stomach oil) removed from chick stomachs after single feeds on 23 chick nights averaged 4.41 g. Of this mass an average of 2.45 g was free lipid (Table 2). There were no significant differences in either mean stomach oil mass or mean free lipid mass among any of the three nights. The overall mean masses represented 35.8% (stomach oil) and 20.5% (free lipid), respectively, of the estimated mean total meal mass. However, these percentages probably underestimate the true fraction of the meal made up of each of these components, since stomach pumping did not remove all of the liquid in the stomach (see METHODS above). Assuming the pumping technique removed 85% of the liquid, the adjusted fractional composition of the average meal would be: stomach oil 42.1%; free lipids 24.1%; solid stomach contents 57.9%.

*Energy density of feeds.* Free lipids obtained

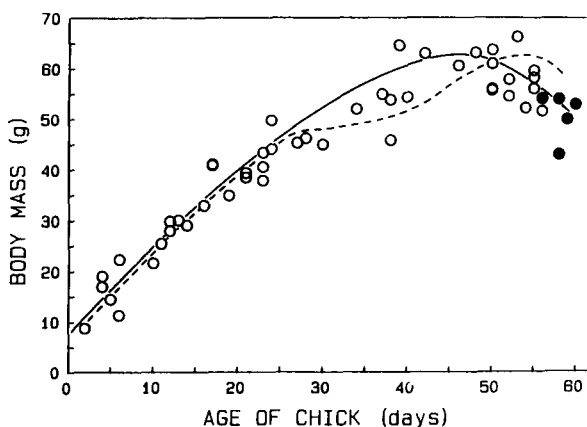


FIGURE 1. Body mass of Wilson Storm-Petrel chicks as a function of estimated age. Open circles represent individuals weighed during the day on Bonaparte Point, Palmer Station, Antarctica. Closed circles represent those individuals that fledged the following night. The solid line was fitted to the data by eye. The broken line represents growth data gathered by Beck and Brown (1972) for the species at the South Orkney Islands.

by centrifugation of stomach oil samples averaged  $40.6 \pm 0.2$  kJ/g ( $n = 9$ ). Solid stomach contents had a mean energy density of  $10.9 \pm 0.3$  kJ/g wet mass ( $n = 9$ ). Assuming that free lipids represent 24.1% and solids 57.9% of the feed mass, the estimated energy density of a typical chick feed would be 16.1 kJ/g of fresh matter, not including any energy-containing substances in the aqueous phase of stomach oil. The mean energy density of five adult regurgitations was 15.5 kJ/g fresh matter, which is 4% below this estimate.

*Chick energy requirements.* Body mass of the chicks increased to a peak of 60–70 g between 45 and 50 days of age and subsequently declined to a mean fledging mass of around 54 g (Fig. 1). Water content increased for the first two weeks, then remained relatively constant (between 18 and 20 ml) until fledging (Fig. 2). Similarly, LDM increased during the chick's first 35 to 40 days, then remained relatively constant through fledging. However, lipid content showed a steady increase to its maximum level at around 50 day, followed by a sharp decrease between 50 day and fledging. Energy content of the chick also peaked around 50 day of age and declined with lipid content thereafter (Fig. 2). The energy content of three fledglings (captured as they emerged from their nest crevices for the first time) averaged 1,101 kJ/bird (889 kJ in lipid and 212 kJ in LFDM). Averaged over a fledging period of 60 days, the net rate of energy deposition in tissues would therefore be 18.4 kJ/day. Peak rates of

energy deposition would be much greater during the period of maximal lipid deposition (between about 25 and 50 days of age), during which lipid content may increase by as much as 1.5 g/day, equivalent to the storage of 57 kJ/day of energy as lipid alone, with more energy undoubtedly being accumulated as protein.

Energy metabolism, measured by  $\text{VO}_2$  at ambient temperatures between 1 and 3°C, rose steadily between day 2 and day 25, was high and relatively constant between day 25 and 50, and showed a decline between day 50 and fledging (Fig. 3). The average rate of energy metabolism, calculated over a 60-day fledging period, was 132.6 kJ/day (Table 3). The mean metabolizable energy requirement of the chick, estimated from the sum of the mean rate of energy deposited in tissues and the mean rate of energy metabolism was 151 kJ/chick·day. Thus, the rates of energy provisioning and energy utilization, which were measured independently, agree within 3%. Estimated energy supply and demand would be equal if the assimilation efficiency were 0.93 rather than the assumed value of 0.90 (above). The value of 0.93 is higher than the range of assimilation efficiencies listed for adult seabirds in recent reviews (0.73–0.85; Adams 1984, Castro et al. 1989, Karasov 1990). However, Obst (1986) found that over 95% of lipid fed to captive adult storm-petrels was assimilated, suggesting that an assimilation efficiency near 90% might be expected for a chick which receives over half of its energy in the form of free lipids. Assimilation

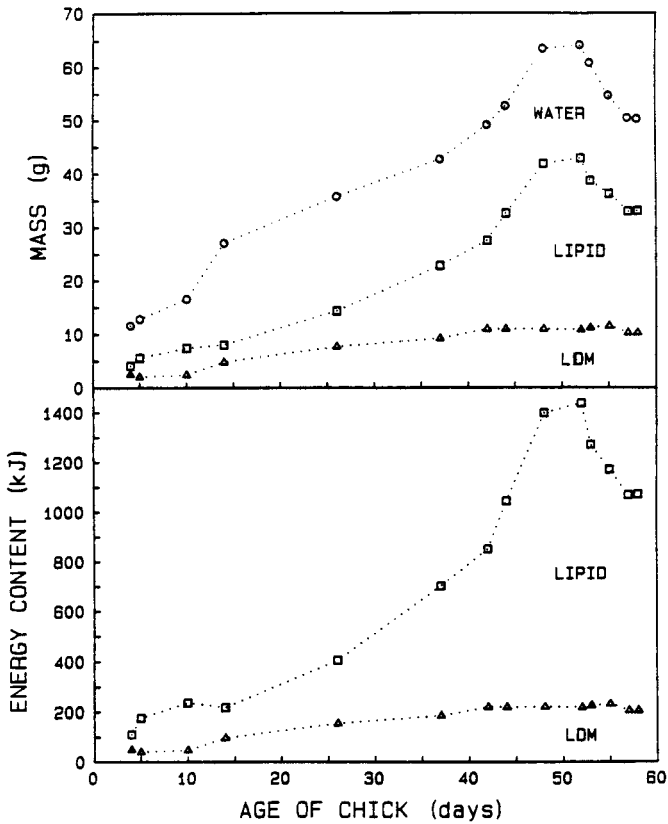


FIGURE 2. Mass and energy contents of Wilson's Storm-Petrel chicks attributable to water, lipid, and lean dry mass (LDM) as a function of estimated age. Data are plotted in a cumulative fashion, such that values along each broken line represent the sum of all the labeled components below.

lation of dietary wax esters by diving petrel, prion, and storm-petrel chicks was near 99% (Roby et al. 1986, Place and Roby 1986).

Although this overall energy budget based upon mean rates of energy input and utilization balances well, daily energy budgets differed, depending on the phase of the nestling period. Mean meal mass did not change significantly as the chicks grew (Fig. 4A). However, the proportion of chicks receiving double feeds declined, while the incidence of no feeds increased through the fledgling period (Fig. 4B). Thus, the net feeding frequency (feeds/chick·night) decreased as the chick grew (Fig. 4C), and the mean mass of food delivered per night tended to decline as the chick grew (Fig. 4D), although differences between the means for the size categories are not significant. The decrease in the feeding frequency is not the result of abandonment of the chicks by the parents. In several instances, chicks were fed on the

same night that they fledged, and parents frequently returned to the nest even after their chick had fledged. Whether parents actually bring fewer feeds to the chick during the late fledging period or whether the chicks simply accept fewer of the feeds offered to them is not known. The period of peak energy metabolism occurred between 31 and 40 days of age when metabolism averaged 160.3 kJ/day.

The average energy requirement of the chick over the 60-day fledging period, estimated from the sum of the mean rate of energy deposition in tissues and the mean rate of energy metabolism, was 151.0 kJ/day (Table 3). Peak energy utilization, falling in the period between 31 and 40 days, was about 217.3 kJ/day.

## DISCUSSION

*Stomach oil and the nestling energy budget.* With the apparent exception of the diving-petrels (*Pe-*

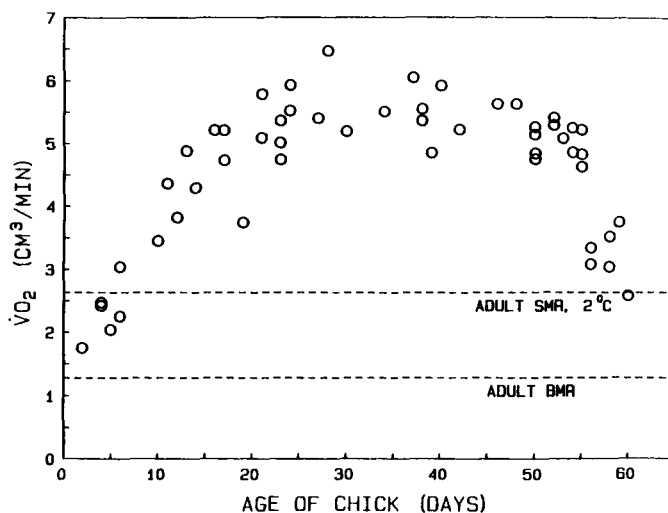


FIGURE 3. Rates of oxygen consumption ( $\dot{V}O_2$ ) in Wilson's Storm-Petrel chicks as a function of estimated age.  $\dot{V}O_2$  was measured at ambient temperatures between 1 and 3°C. Volumes are corrected to units of standard temperature and pressure.

*lecanoides* spp.; Warham 1977), stomach oil comprises a large fraction of the mass delivered by procellariiform birds to their chicks (Ricklefs et al. 1986, Roby et al. 1986, Place et al. 1989, Jackson and Place 1990). A typical Wilson's Storm-Petrel feed contains 42% stomach oil by mass. This value is near the middle of the range of previously published values for other procellariiform species (19–61%; Clarke and Prince 1976, Warham 1977, Jacob 1982, Roby et al. 1986). Because the energy density of the free lipids is high, the stomach oil fraction accounted for an estimated 61% of the total energy delivered in an average Wilson's Storm-Petrel feed. Clearly, stomach oils represent an important source of energy to the growing chick.

A comparison of the estimates of energy supply to, and power and energy demanded by, the chick is instructive. The mean rate of delivery of metabolizable (usable) energy to the nestling can be estimated from the product of the mean meal mass, the mean feeding frequency, the mean energy density of the meal, and the assumed assimilation efficiency of 0.90 for this oily diet:

$$\begin{aligned}
 &(9.2 \text{ g/meal}) \times (1.1 \text{ feeds/chick} \cdot \text{day}) \\
 &\times (16.1 \text{ kJ/g}) \times (0.90 \text{ kJ assimilated/kJ} \\
 &\quad \text{ingested}) \\
 &= 147 \text{ kJ/chick} \cdot \text{day.}
 \end{aligned}$$

If one assumes that the energy density of the meals does not change through the fledging pe-

riod, a more detailed nestling energy budget can be constructed using the mean rates of food delivery from Figure 4D. The gross power delivered to the chick averages 203 kJ/chick·day for chicks between 25 and 35 g, and declines to an estimated 118 kJ/chick·day for the largest chicks (Table 4). The difference between the delivered power and the mean rate of energy metabolism for each size class represents the energy available for deposition in tissues. Assuming that chicks larger than 25 g deposit energy only as fat (Fig.

TABLE 3. Energy utilization by nestling Wilson's Storm-Petrels and Leach's Storm-Petrels.

Chick ages (days)	Metabolic rate (kJ/day)				Ratio Wilson's/Leach's
	Wilson's Storm-Petrel		Leach's Storm-Petrel		
	Mean	SE (n)	Mean	SE (n)	
1–5			26.2	2.65 (10)	
6–10	72.1	6.37 (7)	35.7	2.85 (9)	2.3
11–20	128.1	5.79 (9)	45.6	2.46 (23)	2.8
21–30	157.7	4.63 (10)	61.1	3.18 (25)	2.6
31–40	160.3	4.92 (6)	71.2	2.46 (37)	2.3
41–50	150.8	3.76 (7)	79.2	3.57 (32)	1.9
51–60	125.6	7.24 (15)	78.1	5.88 (13)	1.6
1–60	132.6	(54)	61.0	(150)	2.2
Deposition in tissue					
1–60	18.4		19.1		1.0
Total power requirement (metabolism and tissue)					
1–60	151.0		80.1		1.9

\* All data for Leach's Storm-Petrel are from Ricklefs et al. 1980a.



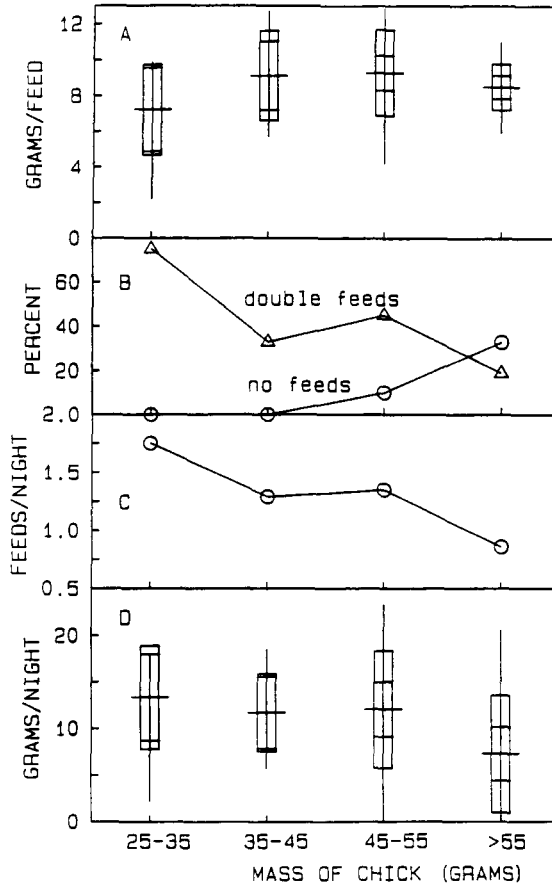


FIGURE 4. Aspects of chick provisioning by Wilson's Storm-Petrel as a function of chick mass: Figure 4A—Feed mass; Figure 4B—The frequency of double feeds (triangles) and no feed (circles); Figure 4C—The average feeding frequency; Figure 4D—Total mass of food delivered per chick, per night. In 4A and 4D, the wide horizontal line represent sample means and the short horizontal lines indicate the 95% confidence limits of the mean. The vertical lines represent the range and the vertical bars span one standard deviation above and below the mean.

2), the rate of fat deposition (g/day) can be predicted by:

$$\frac{(\text{metabolizable kJ/day delivered} - \text{kJ/day respired})}{(38 \text{ kJ/g lipid})}$$

for chicks belonging to size classes 25–35 g, 35–45 g, and 45–55 g (Table 4). These growth rate estimates are very similar to actual growth data for the younger chicks (taken from Fig. 1), but predicted growth rates fall about 0.5 g/day short of actual growth rates of older chicks. Furthermore, an energy shortfall of 43.1 kJ/day is predicted for chicks heavier than 55 g. This should result in a decline in lipid reserves of about 1.1 g/day, in general agreement with the observed

decrease in mass of about 8 g during the 5–10 days prior to fledging.

*Comparison with Leach's Storm-Petrel.* Leach's Storm-Petrel (*Oceanodroma leucorhoa*), is a widely distributed species in the temperate northern hemisphere (Montevecchi et al. 1992), and is very similar to Wilson's Storm-Petrel in body size and many aspects of its breeding phenology (Table 5). The species has been well studied at its breeding grounds on Kent Island, New Brunswick in terms of its growth and development (Ricklefs et al. 1980b), nestling energetics (Ricklefs et al. 1980a), the provisioning of young (Ricklefs et al. 1985; Ricklefs 1987, 1992), stomach oil (Place and Roby 1986, Place et al. 1989),

TABLE 4. Energy budget for nestling Wilson's Storm-Petrels.

	Body mass (g) category			
	25-35	35-45	45-55	>55
Power (gross) delivered to the chick (kJ/day) <sup>a</sup>	203.3	188.9	194.3	117.5
Rate of energy metabolism (kJ/day) <sup>b</sup>	115.5	140.9	145.0	148.8
Predicted rate of energy deposition in tissues (kJ/day) <sup>c</sup>	67.5	29.1	29.9	-43.1
Body mass change rate predicted (g/day) <sup>d</sup>	1.78	0.77	0.79	—
Actual (g/day) <sup>e</sup>	1.67	1.43	1.25	—

<sup>a</sup> Calculated as = (feed mass) × (feeding frequency) × (energy density of the feed).

<sup>b</sup> Measured as  $\dot{V}O_2$  at ambient temperatures between 1 and 3°C.

<sup>c</sup> Calculated as = [(gross power delivered to the chick) × (0.90 kJ assimilated/kJ eaten)] - (rate of energy metabolism).

<sup>d</sup> Calculated as = (predicted rate of energy deposition)/(38 kJ/g). See text for explanation.

<sup>e</sup> Values taken from the growth curve, Figure 1.

and adult energy requirements (Ricklefs et al. 1986). It thus provides an interesting basis of comparison with the high-latitude Wilson's Storm-Petrel.

Air temperatures in the nest burrows of Leach's Storm-Petrels on Kent Island range from 10–15°C, well above the mean air temperature of 2°C measured in Wilson's Storm-Petrel nest crevices at Palmer Station (Fig. 5).  $\dot{V}O_2$  measurements of Leach's chicks in metabolic chambers held at ambient temperatures between 15 and 25°C (Ricklefs et al. 1980a) indicate that rates of energy metabolism average 61 kJ/day, only 46% of the mean value measured at 2°C in Wilson's Storm-Petrel chicks in this study (Table 3). Mean rates of energy metabolism were significantly lower in Leach's than in Wilson's Storm-Petrel for every age group. The mean rates of energy deposition in tissues are nearly identical in the two species between day 1 and day 60 after hatching (19.1 and 18.4 kJ/day for Leach's and Wilson's Storm-Petrel, respectively). The total power requirement of Leach's Storm-Petrel chicks averages 80.1 kJ/day, only 53% of the corresponding value for Wilson's chicks (Table 3). Both species have quite high total metabolizable energy requirements to fledge a chick, being 4.6× higher for Leach's Storm-Petrel than predicted (Weathers 1992) for the fledgling body mass. This is mainly a consequence of the unusually long nestling period of procellariid birds, in general.

How does the chick provisioning strategy of the more temperate Leach's Storm-Petrel compare with that of Wilson's Storm-Petrel? Mean

meal masses of the two species are not significantly different, with adults of both species carrying loads of about 9 g to the nest (Table 6). However, the feeding frequency measured in Wilson's Storm-Petrel was 24% higher than the corresponding value measured in Leach's Storm-Petrel. Ricklefs et al. (1985) reported that Leach's chicks were not fed on 56 out of 161 chick nights. This frequency is significantly higher than that of Wilson's Storm-Petrel reported in this study ( $\chi^2 = 4.26$ ;  $df = 1$ ;  $P < 0.05$ ). Furthermore, the energy density of the meals in Wilson's Storm-Petrels (16.1 kJ/g) was also higher than that reported for Leach's (12.6 kJ/g; Ricklefs et al. 1986). Calculating the mean gross power delivered to Leach's Storm-Petrel chicks, as was done above for Wilson's, one finds:

$$(8.56 \text{ g/feed}) \times (0.82 \text{ feeds/day}) \times (12.6 \text{ kJ/g}) \\ = 88.4 \text{ kJ/day.}$$

This estimate agrees reasonably well with the estimated gross power requirement of 80.1 kJ/day. The ratio of power utilized to gross power

TABLE 5. Aspects of the breeding biology of Wilson's Storm-Petrel and Leach's Storm-Petrel.

	Wilson's Storm-Petrel	Leach's Storm-Petrel
Body mass	42	45
Clutch size	1	1
Egg mass (g)	11.0	10.7
Hatchling mass (g)	8.0	7.3
Incubation period (days)	42	42
Fledging period (days)	52–60	63–70
Fledgling mass (g)	55	60

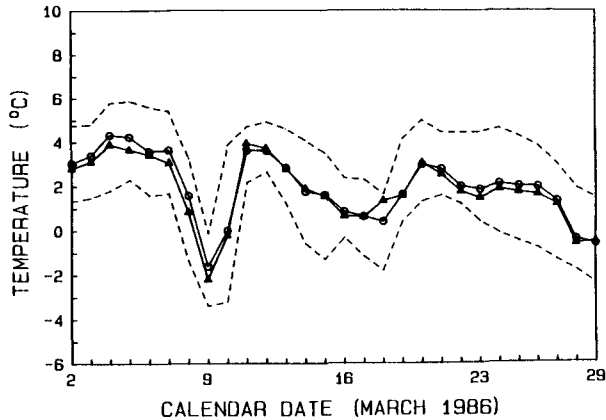


FIGURE 5. Air temperatures inside nest crevices of Wilson's Storm-Petrels on Bonaparte Point, Palmer Station, Antarctica. Circles represent the mean daily air temperature averaged for five nests. Triangles represent mean daily shaded-air temperatures. The broken lines represent the extreme range of temperatures (maximum high and minimum low) recorded in the nest crevice each day.

delivered is  $80.1/88.4 = 0.91$ , which is very similar to the corresponding ratio in Wilson's Storm-Petrel chicks (0.93), and suggests an overall assimilation efficiency of 0.91 for Leach's Storm-Petrel chicks. Thus, it appears that Wilson's Storm-Petrel meets the higher energy demands of their chick by delivering more feeds of similar size but higher energy content, when compared to the more temperate latitude Leach's. What might the energetic costs of such a strategy be?

Rates of energy metabolism (i.e.,  $\text{CO}_2$  production) have been measured for both Wilson's (Obst et al. 1987) and for Leach's Storm-Petrels at a Bay of Fundy colony (Ricklefs et al. 1986) and at a Newfoundland colony (Montevecchi et al.

1992) during chick-rearing, using the doubly labeled water method. Wilson's Storm-Petrels expend an average of 157 kJ/day while foraging for the chick, 29% above the corresponding Leach's value of 122 kJ/day at the Bay of Fundy, but essentially the same as the Leach's value of 161 kJ/day at Newfoundland. This difference may be a consequence of relatively greater thermoregulatory costs, higher levels of activity, or some combination of these factors. While away from the nest, Wilson's Storm-Petrels appear to fly nearly continuously (Obst et al. 1987), whereas Leach's may sit on the water to feed and rest (Ricklefs et al. 1986). Pennycuik (1982) reported a mean flight speed for Wilson's Storm-Petrel at South Georgia of 10.5 m/sec, a value well above the calculated velocity for minimum power expenditure (5.6 m/sec) but comparable to the calculated velocity for achievement of maximum range (9.9 m/sec). It is tempting to speculate that the high energy requirements of the chick may have selected for a provisioning strategy that relies upon energetically-expensive foraging in adults, a strategy in which fast and continuous flight allow large areas of the ocean to be searched for food. It will be informative to determine whether the difference in foraging metabolic rates of the two populations of Leach's Storm-Petrels is due to thermoregulatory expenses of the adults, as suggested by Montevecchi et al. (1992), or to differences in foraging behavior that may be necessitated by differing chick food requirements. This question is especially interesting, because

TABLE 6. Aspects of chick provisioning by Wilson's Storm-Petrel and Leach's Storm-Petrel.

	Wilson's Storm-Petrel <sup>a</sup>	Leach's Storm-Petrel	Ratio Wilson's/Leach's
Mean feed mass (g/feed)	9.18	8.56	1.07
Feeding frequency (feeds/chicks·day)	1.10	0.82	1.34
Energy density of feed (kJ/g)	16.1	12.6	1.28
Power delivered to chick (kJ/chick day) <sup>c</sup>	162.6	88.4	1.84
Adult's power requirement during foraging (kJ/day)	157	122	1.29

<sup>a</sup> Data from this study and Obst (1986).

<sup>b</sup> Data from Ricklefs et al. (1980a), Ricklefs et al. (1985), and Ricklefs et al. (1986).

<sup>c</sup> Calculated from the product of feed mass, feeding frequency, and energy density of the feed.

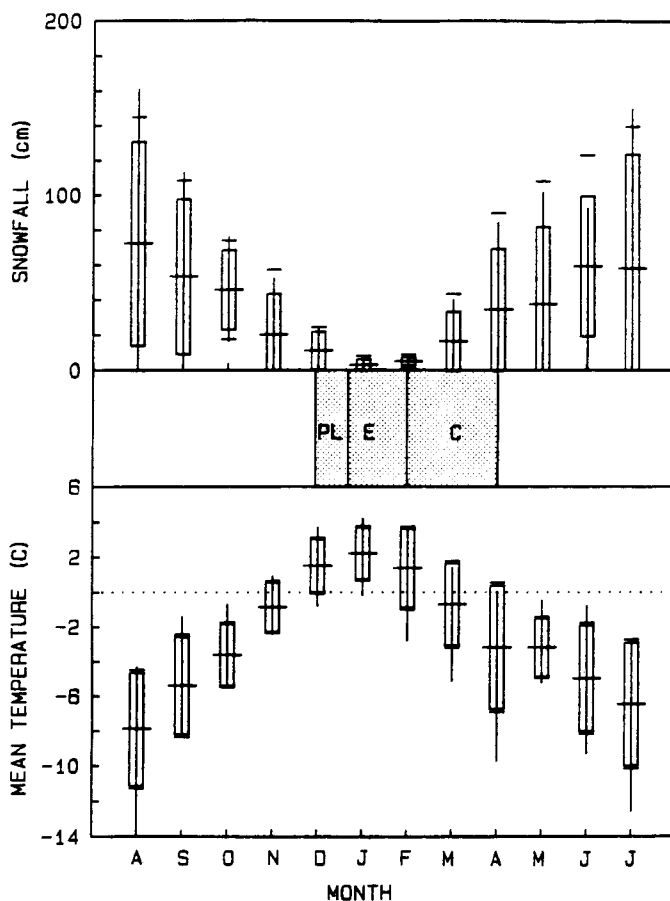


FIGURE 6. The timing of the breeding cycle in relation to the annual climate at Palmer Station, Antarctica. Data for snowfall and air temperatures come from five years (1980–1985) of quarterly weather summaries published in the Antarctic Journal of the United States. Abbreviations are: PL = pre-laying period; E = egg present in nest; C = chick present in nest. Symbols are as described in Figure 4.

Ricklefs (1987, 1992) has shown that Leach's Storm-Petrel parents at the Bay of Fundy do not increase food delivery in response to increased food demand by chicks.

*Evolutionary considerations.* From a comparative study of the sympatric Black-browed Albatross (*Diomedea melanophris*) and Grey-headed Albatross (*D. chrysostoma*), Prince (1985) concluded that the slower growth of *D. chrysostoma* could be attributed in part to the adults' selection of prey with a relatively low energy density. The long fledging period in turn constrained *D. chrysostoma* adults to breed only every second year, rather than every year as in *D. melanophris*. What factors might have selected for a strategy in Wilson's Storm-Petrel requiring high rates of adult energy expenditure rather than the alter-

native strategy of lower power delivery and slower chick growth?

Wilson's Storm-Petrel is an obligate burrow nester, owing to the presence of avian predators in its colonies, including giant-petrels (*Macronectes* spp.), skuas (*Catharacta* spp.) and a gull (*Larus dominicanus*). However, the chief cause of chick mortality at sites north of 60°S latitude is blockage of these burrows by snow, and the subsequent entombment and starvation of the nestling (Roberts 1940; Lacan 1971; Beck and Brown 1972; Obst, pers. observ.). The typical breeding cycle of the species includes a pre-laying period (including a pre-laying exodus by the female) of at least 10 day, a 42 day incubation period, and a 58 day fledging period. Thus, Wilson's Storm-Petrels require a minimum of 110

days to complete their reproductive cycle. Snowfall is variable at Palmer Station from year to year, but a typical annual cycle does exist (Fig. 6). Heavy snows accumulate through the austral winter (May–October), often covering nest crevices. Not until late November, when snowfall begins to decrease and mean daily air temperatures rise above freezing, does the snow blockage begin to disappear. By mid-December, most nests are snow-free and adults have begun to visit them. If the breeding cycle begins at this point, it will not reach its conclusion (with the fledging of chicks) until late March. By late March, and especially by early April, rates of snowfall have begun to increase. Moreover, air temperatures are dropping again to sub-freezing levels such that snows tend to “stick” and accumulate in drifts. Chicks that remain in the nest beyond 1 April are at great risk of entombment. Thus, selective pressure to limit the length of the fledging period should be strong. In fact, Wilson’s Storm-Petrels have perhaps the shortest fledging period among hydrobatids.

The time constraint discussed above also underscores the importance of stomach oil in the reproductive success of this species. In the absence of stomach oil, adult Wilson’s Storm-Petrels would have two evolutionary options: (1) they could deliver energy to the chick at the same rate, by increasing feed size and/or frequency to compensate for the lower energy density of the feed; or (2) they could deliver energy at a lower rate, resulting in a longer fledging period for the chick. Because chick growth rate appears to be constrained by climate, only the first alternative seems viable. However, compensating for the absence of stomach oil would demand shifts in adult behavior that in fact are probably also impossible within the context of the species’ breeding environment.

The mean feed size in Wilson’s Storm-Petrel, 9.2 g, amounts to 22% of the mean adult body mass, a high value for seabirds in general (Ricklefs 1983). The maximum feed mass recorded during this study was ~13 g or 31% of the adult body mass. Assuming this to represent some functional limit of the adult’s capacity, one can calculate the feeding frequency that would be required to maintain the average delivered power measured in this study. Without stomach oil, the energy density of the feed would be near the energy density (metabolizable) of whole prey, i.e., 5.5 kJ/g for krill (Obst et al. 1987). If both parents

were to deliver the maximum feed mass each night, the delivered power would still amount to only  $26 \text{ g/day} \times 5.5 \text{ kJ/g} = 143 \text{ kJ/day}$ . This is just sufficient to meet the requirements for energy metabolism alone in chicks older than 30 days. Thus, without stomach oils, each parent would have to make more than a single trip per day to supply the chick’s energy needs. In reality, such a feeding schedule is not possible. It would require that the adults come and go from the colony during daylight hours, when the risk of predation is extremely high. Thus, because of a set of environmental pressures which include low ambient temperatures, a relatively short season available for breeding, and the presence of avian predators on the breeding grounds, stomach oils represent a key adaptation in Wilson’s Storm-Petrel, contributing to the success of this species in a comparatively hostile environment.

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