SIGNIFICANCE OF STOMACH OIL FOR REPRODUCTION IN SEABIRDS: AN INTERSPECIES CROSS-FOSTERING EXPERIMENT

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ABSTRACT.—Stomach oil, a complex mixture of neutral dietary lipids, is a unique attribute of seabirds in the order Procellariiformes. With the exception of diving-petrels, all procellariiforms produce stomach oil and feed it to their young. We conducted an interspecies cross-fostering experiment on Bird Island, South Georgia, that was designed to reveal how the presence or absence of stomach oil in meals fed to young seabirds influences their growth, development, and survival. Hatchling South Georgia Diving-Petrels (*Pelecanoides georgicus*), a species that lacks stomach oil, were switched with hatchling Antarctic Prions (*Pachyptila desolata*), a species that feeds its young stomach oil. Diving-petrel foster parents did not successfully raise prion nestlings, presumably due to the absence of stomach oil in meals fed to nestlings. Prion foster parents successfully raised diving-petrel nestlings to fledging, but growth rates were lower, nestling fat reserves were lower, and fledging was delayed compared with controls. These results suggest that stomach oil is an essential dietary component for prion nestlings to meet their energy requirements, but diving-petrel nestlings apparently cannot efficiently assimilate stomach oil. This experiment supports the hypothesis that the production of stomach oil is an adaptation that allows breeding seabirds to enhance provisioning rates of energy to the nest, while foraging on a distant and dispersed food supply. *Received 21 October 1996, accepted 15 May 1997.*

A UNIQUE ATTRIBUTE of the breeding biology of members of the Procellariiformes is the storage of significant quantities of neutral lipids in the proventriculus and the feeding of this "stomach oil" to their young. Stomach oil was once thought to be a secretory product (Matthews 1949, Lewis 1966). It is now known to have a dietary origin (Cheah and Hansen 1970, Clarke and Prince 1976, Imber 1976, Warham et al. 1976) and is formed by a combination of specialized gastric anatomy and physiology. The adaptive advantage of stomach oil remains a matter of conjecture (Warham 1977, Jacob 1982).

From the nestling's perspective, stomach oil increases the energy density of meals and meets the nestling's high energy requirements for maintenance (Ricklefs et al. 1980a,b; Simons

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and Whittow 1984). Nestling meals that contain large quantities of stomach oil, however, may be deficient in other nutrients essential for growth and may constrain growth rates (Ricklefs et al. 1987). It is not clear whether the lipid-to-protein ratio of meals containing stomach oil optimizes nestling growth and development or whether it reflects a constraint on adult foraging that imposes additional dietary constraints on nestlings.

Diving-petrels (Pelecanoididae) are the only procellariiforms that do not produce stomach oil (Roby 1989, Warham 1990). Formation of stomach oil in diving-petrels may be precluded by the high rate of energy expenditure of adults at sea (Roby et al. 1989, Taylor et al. 1997). Although low rates of gastric emptying are essential for the formation of stomach oil, they also constrain rates of energy assimilation. Consequently, formation of stomach oil may not be feasible for species with relatively high metabolic energy requirements. Also, formation of stomach oil requires the absorption and excretion of much of the salt load inherent in a zooplankton meal, a mechanism that poses an energetic cost of unknown magnitude (Place et al. 1989).

Cross-fostering experiments have provided one of the most powerful tools for testing hypotheses on the factors constraining reproduction in seabirds. Prince and Ricketts (1981) cross-fostered two closely related species of albatrosses, Black-browed Albatross (*Thalassarche melanophris*) and Grey-headed Albatross (*T. chrysostoma*), which grow at different rates. They showed that interspecific differences in the quality of nestling diets (Clarke and Prince 1980, Prince 1980b) resulted in different growth rates and fledging masses in fostered nestlings compared with controls. These results indicated that the slower growth of Grey-headed Albatrosses was at least partly a consequence of lower diet quality.

Shea and Ricklefs (1985) used cross-fostering to show that adult Gray-backed Terns (*Sterna lunata*) could successfully raise chicks of the larger Sooty Tern (*S. fuscata*) by increasing meal size. They concluded that the slow growth of Gray-backed Tern chicks was not limited by the parents' ability to supply energy to the chick, as suggested by Lack (1968).

We used cross-fostering to evaluate the effects of dietary stomach oil on growth and development of seabird nestlings. Antarctic Prions (*Pachyptila desolata*) and South Georgia Diving-Petrels (*Pelecanoides georgicus*) were selected as subjects for the experiment because both species are small, planktivorous petrels that nest sympatrically on some subantarctic islands (Murphy and Harper 1921; Richdale 1943, 1945, 1965; Tickell 1962). These two species are similar in size, although Antarctic Prions (average adult body mass = 149 g; Taylor et al. 1997) are somewhat larger than South Georgia Diving-Petrels (average adult body mass = 115 g; Roby 1989). Both species raise only a single nestling at a time and parents return to their nest burrows to feed their young only at night (Tickell 1962, Thoresen 1969). Diving-petrels are thought to forage primarily in the neritic zone (Reid et al. 1997), and both parents normally return to the nest site with a meal for their nestling each night (Payne and Prince 1979, Roby 1989). Prion adults return to the nest site less frequently (Taylor et al. 1997) and presumably forage farther offshore. Nestlings of the two species are fed similar amounts of food per day, although South Georgia Diving-Petrel nestlings are fed somewhat more biomass of food on average (43 g/day; Roby 1989) than Antarctic Prion nestlings (37 g/day; Taylor et al., 1997). Antarctic Prions feed their young meals that consist of about 7 to 8% stomach oil by wet mass (Prince 1980a, Taylor et al. 1997). Diving-petrels do not produce stomach oil, and young primarily are fed fresh euphausiids ("krill") with a lipid content of 3 to 8% of wet mass (Payne and Prince 1979, Roby et al. 1986).

If stomach oil is an essential energy supplement for prion nestlings, then those raised by diving-petrel foster parents should exhibit lower growth rates and delayed fledging. Alternatively, if stomach oil is solely a means of compensating for low nestling provisioning rates, then growth and development of fostered nestlings should not be impaired. If high dietary lipid-to-protein ratios or low feeding frequency limits growth and development, then prion nestlings raised by diving-petrel foster parents should exhibit accelerated development relative to controls. If growth rates, fat deposition rates, and development of diving-petrels are constrained by the parents' ability to deliver energy to the nest site, then diving-petrel nestlings raised by prion foster parents should exhibit higher growth rates, larger fat reserves, and shorter nestling periods than controls. Alternatively, if other factors such as essential nutrients, feeding frequency, or physiological constraints limit growth in diving-petrels, then growth of diving-petrel nestlings raised by prion foster parents should be retarded compared with controls.

The overall objective of our research was to evaluate the significance of stomach oil for reproduction in procellariiforms. Comparisons between control and cross-fostered nestlings of a species that produces stomach oil and one that does not were used to examine the relationship between stomach oil ingestion and the growth, development, and energetics of nestlings.

METHODS AND MATERIALS

Field work was conducted on Bird Island (54°00′ S, 38°02′ W), located at the western end of South Georgia, between 14 January and 2 April 1992. On Bird Island, the nesting chronologies of Antarctic Prions and South Georgia Diving-Petrels are similar, an essential prerequisite for success of an interspecies nestling-fostering experiment. Active prion and diving-petrel nests were located and marked at the head

of North Valley late during the incubation period. Nesting habitat and breeding sites of the two study species on Bird Island are described in Payne and Prince (1979), Croxall and Hunter (1982), and Hunter et al. (1982).

Cross-fostering experiment.—We located and marked 75 active nests of each species. Marked nests were checked frequently during the hatching period; ages of half the nestlings were known to within a day, and ages of the remaining nestlings to within two days. These 75 nests were assigned to either the cross-foster or control group largely at random, although we preferentially cross-fostered pairs of hatchlings of appropriate ages (see below).

Cross-fostering was accomplished by switching young nestlings between 30 pairs of nests as soon as the adults had ceased brooding the nestlings during the day. South Georgia Diving-Petrel nestlings normally are brooded continuously by their parents for 6 to 8 days posthatching, and Antarctic Prion nestlings are brooded continuously for only 0 to 3 days (Ricklefs and Roby 1983). Consequently, diving-petrel nestlings were cross-fostered at about 9 to 10 days posthatching with prion nestlings at about 3 to 5 days. The two species are similar in body size and appearance at these respective ages. Switching of nestlings occurred during the day, when both parents were at sea. Previous switching experiments with other closely related species pairs had indicated that parents do not distinguish between their own and cross-fostered nestlings, and that nestlings will accept food from adults of a different species (Prince and Ricketts 1981, Shea and Ricklefs 1985, Roby and Lance 1994). A pilot attempt to cross-foster two pairs of chicks of the study species on Bird Island in a previous year revealed that at least one pair of cross-fostered chicks survived for an extended period under the care of their foster parents (P. A. Prince pers. comm.).

Growth rates of control and cross-fostered nestlings were monitored by weighing and measuring known-age individuals until each nestling fledged, disappeared, or was found dead in the nest burrow. Nestlings were weighed every five days beginning on day 0 (hatching day) using Pesola spring scales (50, 100, or 300 g). We measured wing length and fifth primary length ($\pm$ 1 mm) beginning at day 15 for diving-petrels and day 20 for prions, the approximate ages, respectively, when primaries first erupt in the two species. We used stopped metal rulers to measure wing length and clear plastic rulers to measure fifth-primary length. Because sample sizes of fostered nestlings were smaller than those of controls, we weighed and measured each fostered nestling twice as frequently as control nestlings (i.e. at ages 10, 12, 15, 17, 20, 22, 25, 27, etc. days posthatching).

Feeding rates of small samples of fostered diving-petrels and fostered prions were measured on two consecutive nights using the overnight weighing technique (Ricklefs 1984a, Ricklefs et al. 1985) and compared with those of control prions (Taylor et al. 1997) and control diving-petrels (Roby 1989). A detailed description of the method is presented by Taylor et al. (1997). Briefly, nestlings were weighed in the evening before adults returned to the nest at night to provision their young and at 3-h intervals thereafter until dawn when adults returned to sea. The sum of the positive mass increments during overnight weighing was used as an index to the amount of food fed to the nestling by its parents.

Volume of stomach oil in nestlings.—We measured the volume of stomach oil (liquid lipids) in control and cross-fostered nestlings by dilution of tritium-labeled glycerol triether ([³H]-GTE), a nonassimilable, nonmetabolizable lipid-phase marker (see Morgan and Hofmann 1970; Place et al. 1989, 1991). Briefly, we fed nestlings the marker in an oil carrier, and after an equilibration period of at least 1 h we sampled a small amount of the proventriculus contents (see Taylor et al. 1997). The volume of stomach oil in each nestling was calculated from the expression:

$$(V_s \, C_i / C_s) - V_i, \qquad (1)$$

where V_s is the counted sample volume, V_i is the volume of fed marker solution, C_i is disintegrations/min (DPM) in the fed solution, and C_s is the DPM in the sample removed from the proventriculus.

Nestling fat reserves.—Fat reserves of cross-fostered and control nestlings were estimated nondestructively using total body electrical conductivity (TOBEC) body-composition analysis. Nestling and fledgling fat reserves were measured noninvasively using an EM-Scan SA-2 Small Animal Body Composition Analyzer (EM-Scan Inc. 1991). Nestlings were removed from the nest burrow during the day when the parents were at sea, transported to the field station where TOBEC was measured immediately (within 1 h of removal from the nest burrow), and returned to the nest burrow before dusk.

The TOBEC method relies on the major difference in conductivity between lipids and other body constituents to estimate total lean body mass (Pethig 1979, Van Loan and Mayclin 1987). The difference between total body mass, as determined by weighing, and lean body mass, estimated from TOBEC, provides an estimate of total body fat. Validation studies to date indicate that the accuracy of TOBEC-estimated lean mass can be high ($r^2 = 0.996$) if care is taken to insure that subjects are: (1) properly positioned in the chamber, (2) not hyperthermic, and (3) normally hydrated (Bracco et al. 1983, Walsberg 1988).

Following a protocol developed by Walsberg (1988), nestlings were immobilized by placing them in a nylon stocking. Core body temperature of each subject was measured ($\pm$ 0.1°C) using a BAT-12 thermocouple thermometer by inserting an esophageal probe into the proventriculus. Subjects were then

placed on a plastic (i.e. nonconductive) carrier, secured with rubber bands, and positioned in the sample chamber so that the center of the torso was in the center of the chamber. The SA-2 was used in fixed mode (EM-Scan Inc. 1991), and at least six replicate TOBEC measurements were recorded for each nestling. The position of each subject was changed slightly several times between TOBEC measurements in order to assure that peak TOBEC number was recorded. TOBEC number was calculated as the mean of the highest measurements that were in a series of similar values. Isolated outliers or measurements made while the subject was moving were not included in the analyses. This protocol was designed to minimize error associated with variation in the position of subjects in the chamber.

Use of the TOBEC technique for estimating total body fat of live subjects requires that a calibration curve be developed for each species of interest (Asch and Roby 1995). In addition, it is necessary for the accuracy of the technique to avoid extrapolating from calibration curves derived for adults to young of the same species that have very different body sizes. TOBEC calibration curves were not available for either study species, so samples of nestlings that were sacrificed for other objectives were used to develop calibration curves. In each case, the predictive models for total body fat were derived by regressing total body fat (dependent variable), as determined by proximate analysis of carcasses, against TOBEC number and live body mass (independent variables) in a stepwise multiple regression (Morton et al. 1991, Skagen et al. 1993).

Following measurement of TOBEC in the live subjects that were used to derive calibration curves, subjects were quickly and humanely sacrificed by diethyl ether inhalation. Subjects were weighed (± 0.01 g) on a top-loading balance, placed in plastic bags, and frozen at −20°C for later analysis in the lab. In the lab, subjects were partially thawed, plucked, reweighed, and then dried to constant mass in a convection drying oven at 60°C. Dried carcasses were reweighed to determine moisture content by subtraction and then ground and homogenized in a small electric meat grinder. Aliquots of dried homogenate (2 to 3 g) were extracted to determine fat content of carcasses using a Soxtec HT-12 soxhlet apparatus and petroleum ether as the solvent (Dobush et al. 1985).

Our research followed guidelines set forth by the Institutional Animal Care and Use Committee (ACUC) and the American Ornithologists' Union's Report of the Committee on Use of Wild Birds in Research (*Auk* 105:1A-41A, 1988). The ACUC at Southern Illinois University at Carbondale reviewed the protocol and gave its approval.
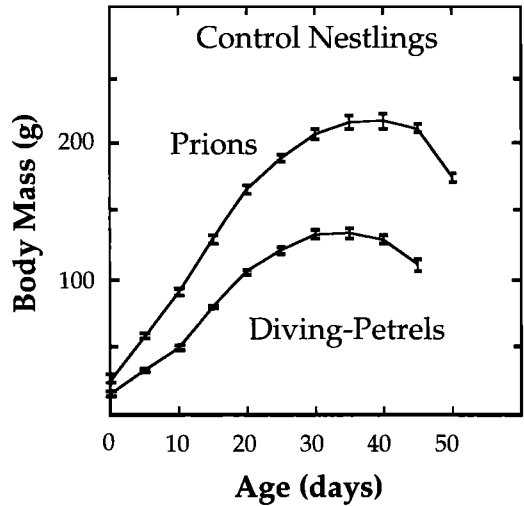

FIG. 1.   Growth in body mass of South Georgia Diving-Petrel and Antarctic Prion nestlings raised in their own nest burrows by their parents (controls) during the 1992 breeding season at Bird Island, South Georgia. Bars are ± 1 SE of each age-specific mean. See Appendix for sample sizes.

RESULTS

Growth of control nestlings.—The pattern of growth in body mass differed between controls of the two study species (Fig. 1; see Appendix for age-specific body mass for control nestlings of the two species). Antarctic Prion nestlings grew at a higher rate, reached higher peak nestling mass, had a more pronounced prefledging mass recession, and fledged at an older age and a greater body mass than South Georgia Diving-Petrels. These differences in part are due to the fact that prions are larger than diving-petrels (mean body mass = 149 g vs. 115 g, respectively). The peak nestling mass of prions (215.9 ± SD of 30.2 g at 40 days, $n = 30$) was, however, greater than that of diving-petrels (133.7 ± 20.2 g at 35 days, $n = 31$) relative to adult mass (145% vs. 116%, respectively). Presumably, this reflects the deposition of larger fat reserves by prion nestlings.

Growth of cross-fostered nestlings.—Less than half ($n = 14$) of cross-fostered prions ($n = 30$) survived to the age of 10 days. Subsequent mortality of the surviving cross-fostered prions was comparatively low until about 30 days, after which their condition deteriorated. None survived to the average fledging age of control prions (ca. 52 days), because all had to
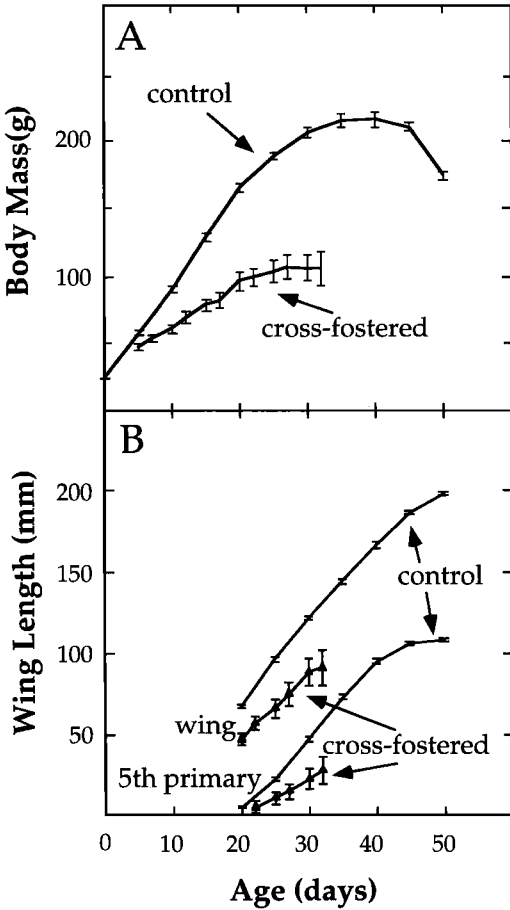
FIG. 2.   Growth in body mass (A) and wing length and fifth-primary length (B) of Antarctic Prion nestlings raised by South Georgia Diving-Petrel foster parents (cross-fostered) compared with control prion nestlings. Bars are ± 1 SE. Sample sizes of cross-fostered prion nestlings are as follows (age in days/n): 5/24, 7/19, 10/14, 12/14, 15/13, 17/13, 20/13, 22/13, 25/12, 27/11, 30/10, 32/8.
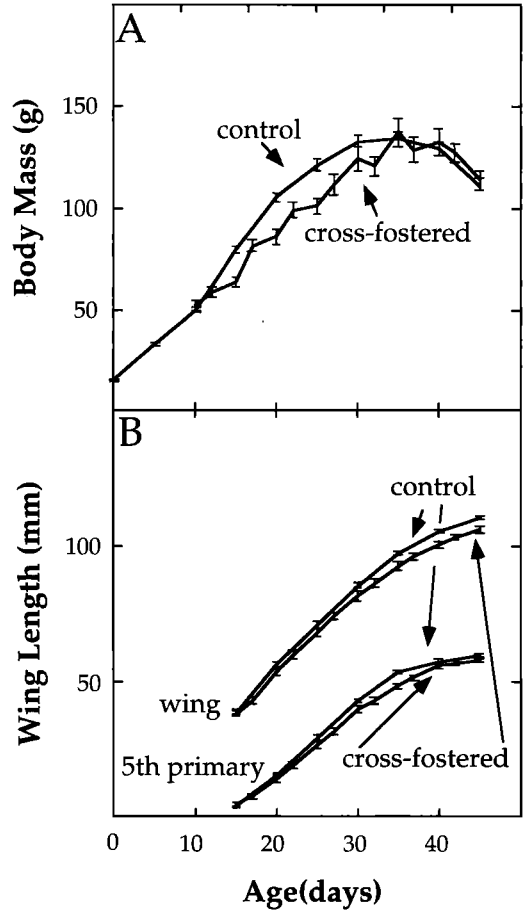
FIG. 3.   Growth in body mass (A) and wing length and fifth-primary length (B) of South Georgia Diving-Petrel nestlings raised by Antarctic Prion foster parents (cross-fostered) compared with control diving-petrel nestlings. Bars are ± 1 SE. Sample sizes of cross-fostered diving-petrel nestlings are as follows (age in days/n): 10/24, 12/29, 15/27, 17/25, 20/24, 22/24, 25/21, 27/20, 30/19, 32/18, 35/18, 37/18, 40/18, 42/17, 45/16.

be euthanized by age 40 days. Growth rate of total body mass in cross-fostered prions was much lower than in control prions (Fig. 2A). Cross-fostered prions appeared to reach an asymptotic body mass of about 100 g by about 20 days posthatching. The dramatic differences in growth of body mass also were apparent in growth of wing length and fifth primary length (Fig. 2B). Average wing length of cross-fostered prions was consistently less than that of controls (t-values = 6.88 to 7.48 for compari-

sons at 20, 25, and 30 days posthatching; $Ps <$ 0.00001).

In contrast, most cross-fostered diving-petrels (17 of 30; 57%) survived until fledging age (ca. 45 days), and their body mass at that age (113.8 ± 16.5 g, n = 13) was similar to that of controls (110.8 ± 14.5 g; t = 0.47, n = 11, P = 0.64). There were, however, differences in growth and development between control and cross-fostered diving-petrels (Figs. 3A, B). Growth in body mass of fostered diving-petrels lagged behind that of controls. At ages 15,

20, and 25 days, fostered diving-petrels had significantly lower body mass than controls ($P < 0.0005$ for each of three t-tests; Fig. 3A). By age 30 days, fostered diving-petrels (124.0 ± 24.3 g, $n = 16$) were no longer significantly lighter than controls (132.5 ± 18.0 g, $n = 39$; $t = 1.44$, $P = 0.156$).

Wing length of fostered diving-petrels was not different from controls on day 15 ($P = 0.76$), day 20 ($P = 0.12$), or day 25 ($P = 0.11$) but was significantly less than controls on day 30 ($P = 0.025$), day 35 ($P = 0.001$), day 40 ($P = 0.0006$), and day 45 ($P = 0.002$). Although age-specific means for wing length of fostered diving-petrels were significantly less than controls late in the nestling period, the actual differences between means were small (Fig. 3B). Finally, 94% of surviving fostered diving-petrels (16 of 17) fledged after age 45 days, whereas only 41% of control diving-petrels (12 of 29) fledged after 45 days. Indeed, fostered diving-petrels fledged at a significantly older age compared with controls ($\chi^2_c = 10.4$, $P = 0.0013$). The later fledging of fostered diving-petrels probably was related to lower rates of wing growth.

We estimated the mass of food delivered per night to fostered diving-petrels by their prion foster parents from the sum of positive mass increments recorded overnight at 3-h intervals (SUM; after Ricklefs 1984a). Nine fostered diving petrels were weighed overnight on two consecutive nights (4 and 5 March) for a total of 18 nestling nights. The average age of these nestlings was 32 ± 3.7 days ($n = 18$), close to the age of peak nestling mass. The average SUM for this sample of fostered diving-petrels (22.1 ± 15.62 g, range 0 to 45 g, $n = 18$) was not significantly different from the average SUM for control prion nestlings (31.3 ± 23.4 g, $n = 57$), but the variance in SUM was high for both samples, and sample size for fostered diving-petrels was small, resulting in low power to detect a difference if present. Average NET (i.e. mass change over 24 h due to the previous night's feeding) of fostered diving-petrels (-1.33 ± 17.31 g, $n = 18$) was not different from 0 or the average NET of control prion nestlings (2.0 ± 13.99 g, $n = 34$), but sample size for the former was small and variance in NET was high. The regression equation of NET on SUM was:

$$NET = -11.38 + 0.511(SUM) \qquad (2)$$

($r^2 = 0.59$, $F = 18.85$, df = 1 and 13, $P = 0.0008$, SE of slope = 0.118).

Five cross-fostered prions also were weighed on the same two nights; the average SUM of this small sample was 20.7 ± 9.46 g (range 9 to 42 g, $n = 9$ nestling nights). The corresponding value for NET was −0.25 ± 5.75 g ($n = 8$ nestling nights), also not different from 0. The regression equation for NET on SUM was:

$$NET = -9.74 + 0.444(SUM) \qquad (3)$$

($r^2 = 0.58$, $F = 8.24$, df = 1 and 6, $P = 0.028$, SE of slope = 0.155).

The only available SUM and NET data for control diving-petrels were collected at the same study site during the 1982 breeding season (Roby 1989). Growth rates of control diving-petrel nestlings in 1992 (Appendix) and 1982 (D. Roby unpubl. data) were quite similar, suggesting that average provisioning rates to diving-petrel nestlings were similar in the two years. The average SUM for control diving-petrel nestlings in 1982 was 41.6 ± 11.4 g, and the average NET was 0.69 ± 6.7 g ($n = 78$ nestling nights). Although the average value of NET was similar between control diving-petrels and fostered prions, the average value of SUM for the small sample of fostered prions was only about half that of control diving-petrels (20.7 g vs. 41.6 g).

An analysis of covariance revealed that the slope of the regression of NET versus SUM for fostered diving-petrels (0.511) was significantly greater ($F = 6.67$, df = 1 and 54, $P = 0.013$) than the slope of the regression for control diving-petrels (0.251; data from 1982). This supports the assumption that prion parents fed stomach oil to fostered diving-petrel nestlings, resulting in a higher conversion efficiency of food to nestling body mass compared with controls. The higher slope of NET versus SUM for fostered diving-petrels was not an artifact of using younger nestlings in the analysis; on average, fostered diving-petrels in this sample were older (32 days) than control diving-petrels (25.7 ± 7.37 days, $n = 78$).

Volume of stomach oil in nestlings.—Volume of stomach oil was measured in control prions ($n = 44$), control diving-petrels ($n = 17$), fostered prions ($n = 8$), and fostered diving-petrels ($n = 15$) using the GTE dilution technique. The experimental error in this technique averaged ± 3.5% (Place et al. 1991), so measured stomach-

oil volumes of <0.1 mL are not different from zero. The distribution of stomach-oil volumes in control prion nestlings was highly skewed, with most individuals containing little stomach oil and only a few storing 5 to 15 mL (Taylor et al. 1997). Stomach-oil volume of fostered prions (median = 0.02 mL, range 0 to 0.21 mL) was lower than that of control prions (median = 0.87 mL, range 0 to 14.07 mL; Mann-Whitney $U = 73.5$, $P = 0.009$). Stomach-oil volume of fostered diving-petrels (median = 0.03 mL, range 0 to 5.05 mL) was not different from that of control diving-petrels (median = 0.00 mL, range 0 to 0.17 mL; $U = 93.0$, $P = 0.193$). Three fostered diving-petrels, however, had measurable volumes of stomach oil (>0.1 mL), whereas no control diving-petrels had detectable amounts of stomach oil. Fostered diving-petrels nevertheless had significantly lower amounts of stomach oil than did control prions ($U = 198$, $P = 0.021$). Therefore, no nestlings fed by diving-petrel parents had measurable volumes of stomach oil, whereas nestlings fed by prion parents did. Of the nestlings fed by prion parents, few diving-petrels (20%) stored measurable amounts of stomach oil, whereas the majority (61%) of control prions did.

Nestling fat reserves.—We collected samples of 45-day-old control ($n = 7$) and fostered ($n = 8$) diving-petrels to test the hypothesis that differences in diet resulted in differences in body composition of nestlings at the age of fledging. Although control diving-petrel fledglings had higher average total body mass, lean body mass, lean dry mass, total body fat, and percent fat of total body mass compared with fostered diving-petrel fledglings, all differences were small and not significant (*t*-tests, $P \geq 0.38$).

Potential differences in body composition of control and cross-fostered nestlings were further investigated using estimates of body composition obtained through TOBEC analysis. Three different TOBEC calibration curves for predicting total body fat from TOBEC number were developed: (1) for nestling South Georgia Diving-Petrels near the age of peak body mass (30 to 35 days posthatching), (2) for fledgling South Georgia Diving-Petrels (ca. 45 days), and (3) for nestling Antarctic Prions near the age of peak body mass (35 to 40 days). Two independent variables (TOBEC number and live body mass) explained a significant proportion of the variation in total body fat and entered the step-

wise regression used to derive each of the three calibration curves. Subject body temperature did not enter the regression models. The calibration equation for nestling South Georgia Diving-Petrels at the age of peak body mass (ca. 30 days) was:

$$\text{Total body fat} = -35.9 + 0.725 \text{ (Live body mass)} - 0.178 \text{ (TOBEC number)} \quad (4)$$

(F-ratio = 23.54, df = 2 and 13, $r^2 = 0.784$, $P < 0.0001$; mean error = 13.5%, range 3.3 to 70.5%). The calibration equation for fledgling South Georgia Diving-Petrels (ca. 45 days) was:

$$\text{Total body fat} = -28.2 + 0.588 \text{ (Live body mass)} - 0.093 \text{ (TOBEC number)} \quad (5)$$

(F-ratio = 111.1, df = 2 and 12, $r^2 = 0.949$, $P < 0.0001$; mean error = 6.9%, range 0.2 to 18.2%). The calibration equation for nestling Antarctic Prions at the age of peak mass (ca. 35 days) was:

$$\text{Total body fat} = -41.055 + 0.949 \text{ (Live body mass)} - 0.42 \text{ (TOBEC number)} \quad (6)$$

(F-ratio = 69.43, df = 2 and 13, $r^2 = 0.914$, $P < 0.0001$; mean error = 7.2%, range 1.0 to 15.8%). In all three cases, error was calculated using the formula:

$$|F - PF|/F \times 100, \quad (7)$$

where F is total body fat (g) and PF is predicted total body fat from the TOBEC calibration equation.

TOBEC number and live body mass were measured on a sample of 37 diving-petrel nestlings (17 control, 20 fostered). The average age of these nestlings was 31.1 ± 1.71 days (range 26 to 36), and there was no difference between the average age of control and fostered nestlings ($t = 1.13$, $P = 0.27$). There was, however, a significant difference between the live body mass of control nestlings (137.2 ± 18.45 g) and fostered nestlings (120.4 ± 16.72 g; $t = 2.91$, $P = 0.0063$). Total body fat was then estimated for each nestling using the appropriate TOBEC calibration equation (equation 4). Estimated total body fat was higher in control nestlings (29.8 ± 8.80 g) than in fostered nestlings (19.25 ± 8.09

g; $t = 3.80$, $P = 0.0006$). Percent body fat of live mass was then calculated to compensate for the difference in live body mass between the two groups. Estimated percent body fat of control diving-petrel nestlings (21.3 ± 4.28%) was higher than that of fostered diving-petrel nestlings (15.47 ± 5.32%; $t = 3.62$, $P = 0.0009$).

A sample of eight 45-day-old fostered diving-petrels (i.e. fledglings) was analyzed using TOBEC, and the estimated total body fat of these fledglings was added to those of the sample of 15 diving-petrel fledglings that were used to derive the calibration curve (equation 5). Estimated total body fat of control diving-petrel fledglings (22.42 ± 5.085 g; $n = 7$) still was not different from fostered fledglings (22.97 ± 8.798 g; $t = 0.15$, $n = 16$, $P = 0.879$).

Finally, we measured TOBEC number and live body mass on a sample of 15 prion nestlings (11 control, 4 fostered). The average age of these nestlings was 32.9 ± 3.92 days (range 25 to 41 days), and there was no difference between the average age of control and fostered nestlings ($t = 1.43$, $P = 0.18$). There was a significant difference between the live body mass of control nestlings (185.7 ± 28.46 g) and fostered nestlings (103.6 ± 16.44 g; $t = 5.38$, $P = 0.0001$). Total body fat was estimated for each nestling using the appropriate TOBEC calibration equation (equation 6). Despite small sample sizes, estimated total body fat from TOBEC was much higher in control prion nestlings (42.3 ± 17.11 g) than in fostered prion nestlings (3.71 ± 8.36 g; $t = 4.25$, $P = 0.0009$). Also, estimated percent body fat of control prion nestlings (22.3 ± 6.72%) was much higher than that of fostered prion nestlings (2.6 ± 8.45%; $t = 4.71$, $P = 0.0004$).

DISCUSSION

Growth of control and cross-fostered nestlings.— The results of the cross-fostering experiment are consistent with the hypothesis that stomach oil provides an essential dietary energy supplement for prion nestlings. Prion nestlings that survived the first week under the care of their diving-petrel foster parents grew poorly and appeared to be chronically undernourished. The results do not support the alternative hypotheses that growth of prion nestlings is constrained by either the high dietary lipid-to-protein ratio or the low frequency of meal delivery.

The growth of fostered diving-petrels was retarded compared with that of controls, but at the time of fledging, body size, mass, and composition differed little between control and fostered diving-petrels (Figs. 3A, B). These results support the hypothesis that growth of diving-petrel nestlings is limited by essential nutrients (other than energy), the frequency of meal delivery, or physiological constraints. The alternative hypothesis that growth is limited by the parents' ability to deliver energy to the nest was not supported.

We collected some data on the provisioning rates to fostered diving-petrel and prion nestlings using the overnight weighing technique, but sample sizes were too small to rigorously test the hypothesis that fostered nestlings were provisioned at the same rate as their control counterparts. Evidence suggested that some fostered nestlings were rejected or poorly provisioned by their foster parents immediately after the cross-fostering event, especially fostered prion nestlings. Half of the fostered prion nestlings were dead or in very poor condition within a week of being moved to diving-petrel nests. Also, the limited data available on provisioning rates to fostered prion nestlings ($n = 9$ nestling nights) suggest that at least some of the survivors were not fed as much food as control diving-petrels. Consequently, it is possible that some of the differences in growth between control and cross-fostered prion nestlings resulted from abnormal nestling-feeding behavior on the part of diving-petrel foster parents.

The slope of the regression of NET versus SUM was significantly greater for cross-fostered diving-petrels than for controls, indicating that the former were fed stomach oil by their prion foster parents. Evidence suggested that diving-petrels had difficulty with the stomach oil that their prion parents fed them. During periodic weighing and measuring of fostered diving-petrels, we noticed that the plumage of some nestlings, especially the head and breast feathers, was soiled with stomach oil. Growth in body mass of fostered diving-petrels also was more erratic compared with controls (Fig. 3A), suggesting that occasional delivery of meals especially high in stomach oil, and/or gaps in delivery of food by prion foster parents, were responsible for temporary

reductions in growth rate of body mass. It seems plausible, therefore, that fostered diving-petrels grew more slowly than controls because of physiological constraints in their ability to efficiently digest and assimilate stomach oil, as well as because feeding rates were lower. We found no evidence in support of the alternative hypothesis that essential nutrients other than energy limited the growth of fostered diving-petrels.

Nestling provisioning rates.—South Georgia Diving-Petrel nestlings are fed on average 1.8 meals each night, usually one meal from each parent (Roby 1989), whereas Antarctic Prion nestlings are fed on average 1.1 meals each night (Taylor et al. 1997). Average meal size for diving-petrel nestlings is 23.3 g (Roby 1989), whereas prion nestlings are fed meals that average 31.7 g (Taylor et al. 1997). Consequently, diving-petrel nestlings raised by prion foster parents would, on average, be fed *less* food per day (ca. 17% less) than they normally receive from their own parents. Conversely, prions raised by diving-petrel foster parents would, on average, be fed about 20% *more* biomass of food per day then they normally receive from their parents.

Taylor et al. (1997) estimated that prion parents feed their nestlings an average of 3 mL of stomach oil per day. This amount of stomach oil in prion diets boosts the energy density to about 7.6 kJ/g wet mass, compared with 5.8 kJ/g wet mass for diving-petrel diets that lack stomach oil (Roby 1991). This means that prion nestlings are fed about 280 kJ/day versus about 250 kJ/day for diving-petrels, a difference sufficient for control prions to grow at a higher rate and deposit larger fat reserves than control diving-petrels. Thus, stomach oil appears to be an essential adaptation for enhancing the energy density of nestling meals in petrel species that feed their young less frequently than diving-petrels.

Volume of stomach oil in nestlings.—Results of the GTE dilution-space experiments support the conclusion that adult diving-petrels do not form stomach oil and do not feed stomach oil to their young. The measurement of small amounts of stomach oil (up to 5 mL) in a few fostered diving-petrels suggests that diving-petrels can store stomach oil in their proventriculus if it is a component of their diet. Taylor et al. (1997) reported that the majority of prion

nestling meals do not contain stomach oil. This would explain the unexpectedly low proportion of control prions and fostered diving-petrels with measurable amounts of stomach oil in their proventriculi. It also may explain how prion parents can raise foster diving-petrel nestlings despite the latter's apparent difficulty in digesting and assimilating stomach oil.

Nestling fat reserves.—Estimated total body fat from TOBEC measurements indicated that control diving-petrel nestlings at the age of peak body mass were able to deposit significantly larger fat reserves than fostered diving-petrels. Similarly, control prion nestlings at the age of peak body mass were able to deposit much larger fat reserves than fostered prions (most fostered prions had essentially no fat reserves). The difference between treatments in the fat reserves of diving-petrel nestlings no longer was apparent by the average fledging age (ca. 15 days later). In the intervening period, fostered diving-petrels had deposited more fat reserves, and control diving-petrels had metabolized some of theirs. These results suggest that diving-petrel nestlings seek to achieve a target level of fat reserves prior to fledging. They also suggest that fostered diving-petrels, despite apparent difficulties in adjusting to prion diets and feeding regimes, were able to compensate by late in the nestling period.

Estimates of total body fat also indicated that fat reserves of control prions at the age of peak body mass were very similar to those of control diving-petrels when expressed as a proportion of total body mass (22.3% and 21.3%, respectively). This suggests that prions and diving-petrels have similar target levels for fat reserves, once results are adjusted for differences in body size.

Prions may grow at a higher rate and fledge with larger fat reserves than diving-petrels because dietary stomach oil can meet all of the nestling's energy requirements without catabolizing dietary protein (Roby 1991). This is consistent with the idea that the slow growth of some pelagic seabirds is the result of constraints involving tradeoffs in the management of available energy for reproduction by the parent-offspring unit (Ricklefs 1984b). But it begs the question of why diving-petrels (and other pelagic seabirds) do not feed their young stomach oils. The absence of stomach oil in diving-petrels may be a consequence of higher nest-

ling feeding rates, higher gastric emptying rates, inappropriate gastrointestinal anatomy, or some combination of these factors.

Diving-petrels are pursuit-divers that expend energy at a relatively high rate while foraging (Roby and Ricklefs 1986) compared with prions (Taylor et al. 1997). Taylor et al. (1997) proposed that the high field metabolic rates of diving-petrels preclude the formation of stomach oil and the allocation of this high energy component of the diet to their young. This, coupled with high rates of meal delivery to nestling diving-petrels compared with other procellariiforms, provides an explanation for the absence of stomach oil in the diets of nestling diving-petrels.

For petrels that forage far from the nest site, there is a clear energetic advantage to feeding nestlings a diet that consists largely of stomach oil. By concentrating dietary lipids in the proventriculus, adults can reduce the mass of nestling meals and the frequency of meal delivery, thus lowering the time and energy costs of transporting food from the foraging area to the nest (Ashmole 1971, Laugksch and Duffy 1986, Obst and Nagy 1993). Both breeding and non-breeding adults store stomach oil, however, suggesting that it is not solely an adaptation for reproduction (Jacob 1982). Metabolism of stomach oil at sea may preclude the energy cost of synthesizing fat depots from assimilated fatty acids and of later mobilizing those energy reserves from adipose tissue during fasts, costs that amount to 25 to 30% of the assimilated energy (Ricklefs 1974, Spady et al. 1976). It is likely that these same energy savings confer a benefit to nestlings that store stomach oil in lieu of body fat as an energy reserve.

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APPENDIX. Age-specific body mass ($\bar{x} \pm$ SD) of nestling South Georgia Diving-Petrels and Antarctic Prions (controls only) during the 1992 breeding season on Bird Island, South Georgia. Age is in days posthatching.

Age	Mass (g)	n
South Georgia Diving-Petrel		
0	15.3 ± 2.5	52
5	32.9 ± 5.5	47
10	50.1 ± 10.4	44
15	79.5 ± 11.8	43
20	105.3 ± 15.7	42
25	120.9 ± 18.7	39
30	132.5 ± 18.0	39
35	133.7 ± 20.2	31
40	128.8 ± 18.4	30
45	110.8 ± 14.5	11
Antarctic Prion		
0	25.4 ± 4.8	54
5	58.5 ± 13.2	56
10	90.8 ± 16.7	55
15	129.2 ± 21.7	54
20	165.9 ± 23.8	54
25	188.6 ± 22.6	53
30	205.8 ± 27.4	50
35	214.8 ± 29.4	38
40	215.9 ± 30.2	30
45	210.2 ± 17.2	25
50	174.2 ± 15.3	19