Energetics of nestling growth and parental effort in Antarctic fulmarine petrels

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Summary

Antarctic fulmarine petrels breed in some of the coldest conditions encountered by any bird and their young grow twice as fast as predicted allometrically. To examine the energetic consequences of fast growth in a cold environment, we used the doubly labeled water technique to measure field metabolic rates of adults (three species) and different-aged nestlings (four species) of Antarctic fulmarine petrels in the Rauer Islands, East Antarctica: Antarctic fulmar *Fulmarus glacialoides*, Antarctic petrel *Thalassoica antarctica*, Cape petrel *Daption capense* and snow petrel *Pagodroma nivea*. We used our data to assess parental effort and, together with literature values on nestling growth and resting metabolic rate, to construct and partition nestling energy budgets. Nestling total energy expenditure and peak daily metabolic rate were significantly higher than predicted allometrically (33–73% and 17–66% higher, respectively), and the relative cost of growth in nestling petrels was among the highest reported for birds (54–72 kJ g^{-1}). Parental effort during the nestling-feeding period was identical in adult Cape and Antarctic petrels (3.5 times basal metabolic rate, BMR), and was somewhat (but not significantly) higher in snow petrels (4.6 times BMR). These values are comparable to those of other high-latitude procellariiform birds. Thus, despite the constraints of a compressed breeding season, cold temperatures and fast-growing nestlings, adult Antarctic fulmarine petrels do not work harder than procellariid adults whose chicks grow much more slowly. Our findings suggest that obtaining sufficient food is generally not a constraint for adult fulmarine petrels and that factors operating at the tissue level limit nestling growth rate.

Key-words: doubly labeled water, reproductive effort, field metabolic rate, nestling energy budget, parental effort, Antarctic fulmarine petrel, *Fulmarus glacialoides*, *Thalassoica antarctica*, *Daption capense*, *Pagodroma nivea*.

Introduction

One of the main evolutionary options available to birds for balancing food supply and production is to vary nestling growth rate (Ricklefs et al., 1998). The consequences of growth rate variation on nestling energy requirement is complex, however, and depends upon whether one considers the total energy metabolized during growth or the energy metabolized per day. A reciprocal relationship exists between total metabolizable energy (TME) and daily metabolizable energy (DME), such that nestlings that spend longer in the nest than predicted from their mass generally have lower DME but higher TME values than nestlings that fledge sooner (Weathers, 1992, 1996). Consequently, although lengthening the nestling period decreases the amount of food that parents must provide their nestlings on a daily basis, it increases the total energy required per offspring and thus might negatively impact production at the population level in energy-limited environments.

Antarctic fulmarine petrels are an excellent group in which to investigate linkages between nestling energetics, growth rate, and parental effort. Like other procellariiform seabirds, they exhibit a suite of life-history traits that have long been viewed as adaptations to energy limitation arising from a patchy and unpredictable food supply (Ashmole, 1971) – production of a single chick, slow growth, a long juvenile period and high adult survival (reviewed by Warham, 1990). Yet Antarctic fulmarine petrels differ from most procellariiform species in that their chicks can grow twice as fast as predicted allometrically (Warham, 1990; Hodum, 1999). Furthermore, they breed in some of the coldest conditions encountered by any bird, with air temperatures as low as –25°C (Bech et al., 1988). Relatively fast growth in a cold environment should increase nestling energy demand and concomitantly affect parental provisioning effort.

In this study, we used the doubly labeled water (DLW) technique to measure adult and nestling energy requirements in four of the five fulmarine petrel species that breed in Antarctica: the Antarctic fulmar *Fulmarus glacialoides*, Antarctic petrel *Thalassoica antarctica*, Cape petrel *Daption*

Table 1. *Breeding parameters of Hop Island Antarctic fulmarine petrels*

	Snow petrel	Cape petrel	Antarctic petrel	Antarctic fulmar
Adult mass (g)	264±20 (84)[a]	477±29 (84)[b]	692±52 (50)[c]	858±654 (60)[d]
Incubation period (days)	43.4±1.0 (128)[a]	45.4±1.1 (176)[b]	47.4±1.0 (181)[c]	47.0±1.3 (232)[c]
Nestling period (days)	47.0±1.8 (115)[a]	47.1±1.5 (128)[a]	48.4±2.0 (70)[b]	52.1±1.7 (111)[c]
Breeding cycle (days)	90.3±1.9 (115)[a]	92.5±1.7 (128)[b]	95.9±2.2 (70)[c]	99.2±2.3 (111)[d]

Values are means ± S.D. and are pooled for three consecutive breeding seasons.
Sample sizes are given in parentheses.
Superscripts denote significant differences by row (ANOVA, Tukey: $P<0.05$).

capense and snow petrel *Pagodroma nivea*. We combined our DLW data with information on the growth (Hodum, 1999) and resting energy requirement (Weathers et al., 2000) of nestlings to generate nestling energy budgets and examine the assertion that petrels require considerably more energy to produce 1 g of fledgling than other seabirds (Simons and Whittow, 1984). We also tested the hypotheses that nestling total metabolizable energy requirement should be lower than predicted because of the relatively short nestling period, but that nestling peak daily metabolizable energy requirement should be higher than predicted because of fast growth.

Materials and methods

We conducted our study on Hop Island (68°50′S, 77°43′E) in the Rauer Islands, East Antarctica during three consecutive breeding seasons, 1993–94 through 1995–96. All four species, Cape petrel *Daption capense* L., snow petrel *Pagodroma nivea* Forster, Antarctic petrel *Thalassoica antarctica* Gmelin and Antarctic fulmar *Fulmarus glacialoides* Smith, breed sympatrically on this island, with egg laying from the end of November through mid-December and hatching from the first week in January through early February, depending on species. Conditions on Hop Island are harsh throughout the brief Antarctic summer, with frequent snow, wind and air temperatures below 0°C. Three of the four species nest on the surface (snow petrels nest in rock crevices), and adult body mass ranges from 264 g (snow petrel) to 858 g (Antarctic fulmar). Developmental rates are proportionately faster in the larger surface-nesting species. Consequently, there is much less variation between species in incubation period (43–47 days) and nestling period (47–52 days) than one might anticipate from the threefold range in adult mass (Table 1). Fast growth is at a premium in Antarctica and Antarctic fulmarine petrels compresses the entire breeding cycle into 90–99 days (Table 1), growing up to twice as fast as predicted allometrically (Warham, 1990; Hodum, 1999). For a detailed description of the species' breeding biology and Hop Island's physical characteristics, see Hodum (1999).

We determined nestling and adult field metabolic rates (FMR), using the doubly labeled water (DLW) technique (Tatner and Bryant, 1989). We assessed nestling FMR throughout the entire nestling period, making measurements at 3, 9, 15, 21, 27, 33 and 39 days of age plus, for fulmars only,

45 days of age. We determined FMR of snow petrel (N=50) and Cape petrel (N=51) nestlings during the 1993–94 through 1995–96 seasons and Antarctic petrel (N=21) and fulmar (N=24) nestlings during the 1995–96 season. We marked nests and monitored them daily, and thus knew the exact hatch date and age of all nestlings. No nestling was used more than once. We measured adult FMR during the nestling provisioning period for snow (N=11) and Cape petrels (N=26) during the 1993–94 through 1995–96 seasons and for Antarctic petrels (N=2) during the 1995–96 season. We also determined FMR for incubating snow (N=7) and Cape petrels (N=7) during 1995–96.

To determine nestling FMR, we captured and weighed nestlings at the nest and injected them intraperitoneally with 1 μl g^{-1} body mass of water containing 63 atoms percent ^{18}O and 33 atoms percent ^{2}H. We returned nestlings to the nest for 1 h to allow the injected material to equilibrate with body water (Williams and Nagy, 1984) and then removed blood samples from them (ca. 30 μl collected from a brachial vein). 24 h later, we reweighed the nestlings and took a second blood sample. All injected nestlings were successfully resampled over all three seasons and all were growing normally at the time of injection. We determined natural background isotope abundance in 4–6 uninjected nestlings over 2–3 seasons and used the mean background levels (Table 2) in our CO_2 production calculations.

To determine adult FMR during the nestling stage, we captured adults at the nest after they had fed their chicks, weighed them, collected a blood sample to establish background isotope abundance (ca. 30 μl collected from a web vein in the foot), and then injected them intraperitoneally with 0.45 ml (Cape petrel), 1.0 ml (snow petrel), or 1.5 ml (Antarctic petrel) of water containing 63 atoms percent ^{18}O and 33 atoms percent ^{2}H. After allowing 1 h for the injected material to equilibrate with body water (Williams and Nagy, 1984), we took blood samples from the birds (ca. 30 μl collected from a brachial vein) before returning them to their nest. We recaptured adults at the nest when they returned from their foraging trip, reweighed them, and collected a final blood sample.

To minimize disturbance to incubation-stage adults, we used a single-sample technique (Webster and Weathers, 1989) in which we captured each bird at the nest, weighed and injected it, and returned it to the nest immediately. Approximately 24 h

Table 2. *Background ^2H and ^{18}O isotope levels for nestling Antarctic fulmarine petrels*

Species	δ^{2}H		δ^{18}O	
	Mean	Range	Mean	Range
ANFU (10)	–36.51	–31.74 to –41.49	–0.27	–0.04 to –1.29
ANPE (9)	–37.36	–34.87 to –42.50	–0.91	–0.27 to –1.46
CAPE (15)	–37.58	–30.10 to –43.70	–0.73	–0.06 to –1.54
SNPE (16)	–51.43	–45.62 to –67.57	–1.14	–0.14 to –1.48

δ=[(R_{sample}/$R_{standard}$)–1]×1000, where R denotes isotope ratio.
Sample sizes are given in parentheses.
ANFU, Antarctic fulmar; ANPE, Antarctic petrel; CAPE, Cape petrel; SNPE, snow petrel.

later, we recaptured the bird, reweighed it, and collected a blood sample before again returning it to its nest.

We stored blood samples in flame-sealed hematocrit tubes until they were analyzed for ^{18}O/^{16}O and ^2H/^1H ratios at the Centre for Isotope Research, University of Groningen (Speakman et al., 1990). We calculated rates of water efflux and CO_2 production of adult petrels from isotope turnover using the equations of Lifson and McClintock (1966) as modified by Nagy (1975), and calculated body water volume from ^{18}O dilution following Nagy and Costa (1980). Our CO_2 production calculations took fractionation effects into account by assuming that 25% of water flux represented evaporation (equation 7.17 of Speakman, 1997). We converted CO_2 production of both chicks and adults to energy expenditure in kJ day^{-1} by assuming an energy equivalent of 26.6 J ml^{-1} CO_2 (Ricklefs et al., 1986).

One perennial concern with DLW studies is whether handling alters the animal's behavior and thus might influence its FMR. No measurable behavioral effects were found in green-rumped parrotlets *Forpus passerinus* (Siegel et al., 1999), but substantial changes occurred in the gentoo penguin *Pygoscelis papua* (Wilson and Culik, 1995). To evaluate whether our DLW technique affected adult petrel behavior, we compared foraging trips of experimental birds with those of unhandled controls. All recaptured DLW adults returned with meal sizes that did not differ from those of control birds (*t*-tests: all $P>0.05$). Foraging trip duration did not differ between experimental and control snow petrels ($t_{52}=1.31$, $P=0.20$) or Antarctic petrels ($t_{52}=0.15$, $P=0.88$), but experimental Cape petrels stayed away longer than controls (2.5±0.9 *versus* 1.8±0.6 days, $t_{50}=3.49$, $P=0.01$). There was, however, no correlation between mass-specific FMR and foraging trip duration for either Cape petrels ($r_{24}=0.23$, $P=0.25$) or snow petrels ($r_9=0.16$, $P=0.63$), implying that the longer trip duration of Cape petrels did not influence their FMR.

Nestling energy budgets

We calculated nestling metabolizable energy (ME) as the sum of FMR and the energy retained as new tissue (RE), using our empirically established linear relationships between FMR and mass (Equations 8–11). We assumed ME=FMR during mass recession, which in seabirds represents catabolism of body stores (Roby, 1991). We employed logistic equations for mass *versus* age until peak mass was reached, and linear regression equations to describe mass once mass recession began. We calculated nestling energy content (EC, kJ) using the following equation from Weathers (1996): EC=[3.51+4.82(mM^{-1})]m, where m=wet mass in g for the current day and M=adult mass. We calculated the daily increment in retained energy (RE, kJ d^{-1}) by subtracting the previous day's EC value from the current day's EC. We calculated nestling resting metabolic rate (RMR, kJ d^{-1}) using the following species-specific equations, derived from data of Weathers et al. (2000). (s_{yx} is the standard error of the intercept; s_b is the standard error of the slope.)
Antarctic fulmar:

$$\log RMR = -0.097 + 0.990(\log m) \qquad (1)$$

where $r^2=0.97$, log(s_{yx})=0.070, log(s_b)=0.035, $P<0.001$, $N=30$,
Antarctic petrel:

$$\log RMR = -0.470 + 1.088(\log m) \qquad (2)$$

[$r^2=0.92$, log(s_{yx})=0.103, log(s_b)=0.062, $P<0.001$, $N=30$],
Cape petrel:

$$\log RMR = -0.284 + 1.061(\log m) \qquad (3)$$

[$r^2=0.97$, log(s_{yx})=0.065, log(s_b)=0.039, $P<0.001$, $N=28$],
snow petrel:

$$\log RMR = -0.109 + 0.985(\log m) \qquad (4)$$

[$r^2=0.91$, log(s_{yx})=0.075, log(s_b)=0.060, $P<0.001$, $N=28$], where m is nestling mass in g.

Except where indicated, values are means ± 1 S.D.

Results

Nestling total body water (TBW) content (ml), as determined by ^{18}O dilution, increased linearly with mass for all four species and did not vary between years for Cape and snow petrels. (Antarctic petrels and fulmars were measured during only one field season.) The fraction of nestling mass consisting of water (W_f, ml g^{-1}) decreased linearly with increasing mass (Fig. 1) as described by:

$$W_f = 0.706 - 0.116m \qquad (5)$$

($r^2=0.43$, $s_{yx}=0.050$, $s_b=0.012$, $P<0.0001$, $N=136$), where m is proportion of adult mass attained.

Mass specific water efflux (WE, ml kg^{-1} d^{-1}) was negatively correlated with body mass in nestling snow petrels and Antarctic fulmars (Fig. 2), but not in Cape petrels ($r_{47}=-0.264$, $P=0.064$) or Antarctic petrels ($r_{19}=-0.252$, $P=0.269$). The significant relationships between water efflux and nestling mass are described by the following equations.
Snow petrel:

$$WE = 353.7 - 0.637m \qquad (6)$$

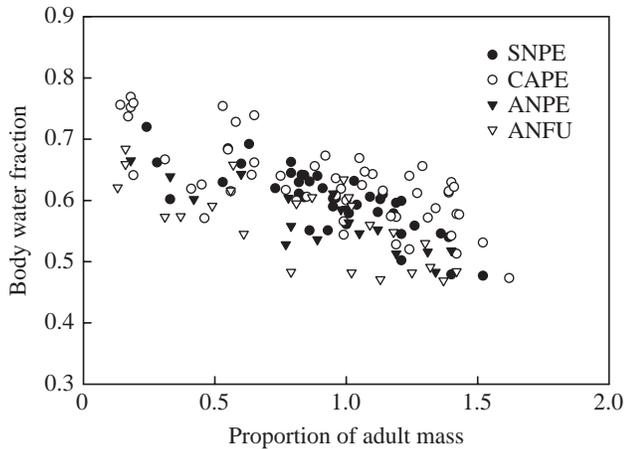($r^2=0.38$, $s_{yx}=61.9$, $s_b=0.118$, $P<0.001$, $N=50$),

Fig. 1. Nestling body water fraction as a function of the proportion of adult mass attained. SNPE, snow petrel; CAPE, Cape petrel; ANPE, Antarctic petrel; ANFU, Antarctic fulmar.
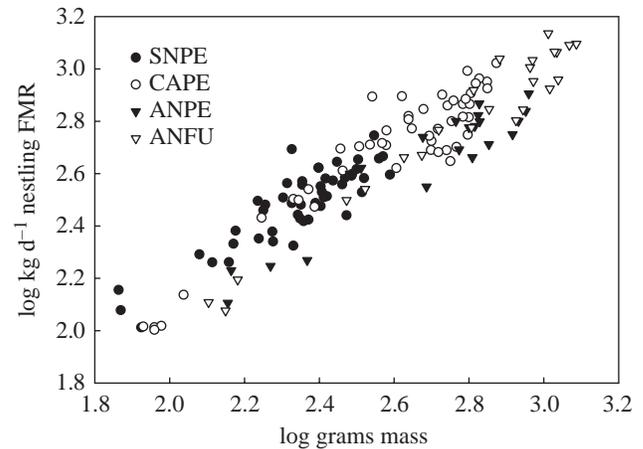

Fig. 3. Log–log plot of nestling field metabolic rate (FMR) as a function of nestling mass. Species abbreviations as in Fig. 1.
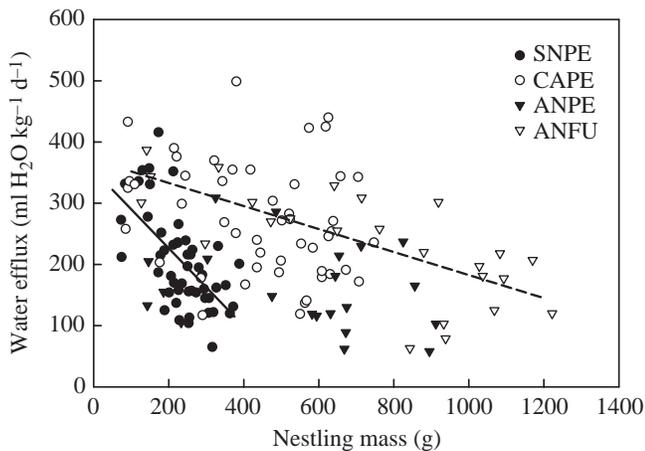

Fig. 2. Water efflux of petrel nestlings as a function of mass. Solid line, SNPE (see text, Equation 6), broken line, ANFU (see text, Equation 7). Species abbreviations as in Fig. 1.

Antarctic fulmar:

$$WE = 371.0 - 0.188m \qquad (7)$$

(r^2=0.52, s_{yx}=63.8, s_b=0.038, $P<0.001$, N=24), where m is nestling mass in g.

The above equations differ in slope (analysis of covariance, ANCOVA; $F_{1,70}$=12.91, $P<0.001$), but not in intercept (ANCOVA; $F_{1,70}$=0.17, $P=0.68$).

Nestling field metabolic rate

Nestling FMR (kJ d^{-1}), calculated from CO_2 production as measured by doubly labeled water, increased with body mass (Fig. 3) as follows.
Snow petrel:

$$\log FMR = 0.576 + 0.81(\log m) \qquad (8)$$

[r^2=0.78, $\log(s_{yx})$=0.073, s_b=0.063, $P<0.001$, N=50], Cape petrel:

$$\log FMR = 0.226 + 0.95(\log m) \qquad (9)$$

[r^2=0.89, $\log(s_{yx})$=0.090, s_b=0.050, $P<0.001$, N=49], Antarctic petrel:

$$\log FMR = 0.332 + 0.86(\log m) \qquad (10)$$

[r^2=0.89, $\log(s_{yx})$=0.081, s_b=0.071, $P<0.001$, N=21], Antarctic fulmar:

$$\log FMR = -0.025 + 1.01(\log m) \qquad (11)$$

[r^2=0.95, $\log(s_{yx})$=0.070, s_b=0.049, $P<0.001$, N=24], where m is nestling mass in g.

Although these equations differ neither in intercept (ANCOVA; $F_{3,132}$=2.48, $P=0.06$) nor slope (ANCOVA; $F_{3,132}$=2.09, $P=0.10$), we used the species-specific relations to estimate nestling FMR in our energy budget calculations, because errors in the TME components are additive.

Nestling mass-specific FMR (kJ g^{-1} d^{-1}) declined with increasing mass in snow petrels (r=0.407, N=49, $P=0.003$) and Antarctic petrels (r=0.483, N=21, $P=0.027$), but not in Cape petrels or Antarctic fulmars (Fig. 4).

Adult field metabolic rate and water flux

Adult Cape and snow petrels both lost significant body mass during the incubation stage, with daily mass losses of DLW birds averaging 5.1 and 6.7%, respectively (Table 3). These mass losses were apparently not fully restored during the incubation recesses when adults fed, because both Cape petrels (t_{31}=4.43, $P<0.001$) and snow petrels (t_{16}=27.7, $P<0.001$) were significantly lighter when feeding nestlings than when incubating eggs. The mass decrease between incubation and provisioning stages averaged 13% and 20%, respectively, for Cape and snow petrels (Table 3).

Adult mass-specific field metabolic rate (ml CO_2 g^{-1} h^{-1}) varied between species and between the incubating and chick provisioning stages of the breeding season (ANOVA; $F_{4,48}$=21.6, $P<0.0001$) (Table 3). Incubating adults had lower
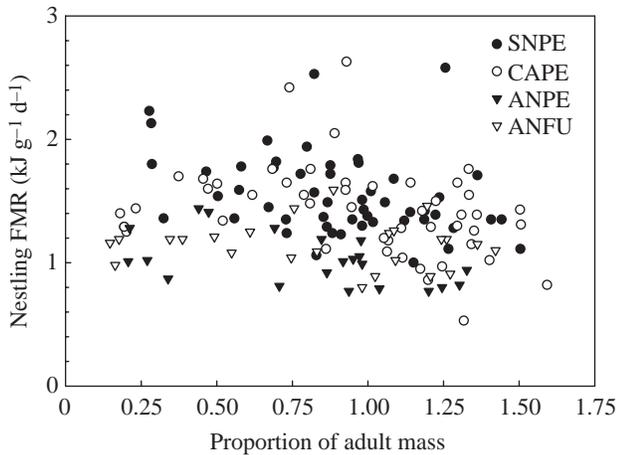
Fig. 4. Mass-specific nestling field metabolic rate (FMR) as a function of the proportion of adult mass attained. Species abbreviations as in Fig. 1.

mass-specific FMR values than adults provisioning nestlings in both snow petrels (t_{16}=6.63, P<0.001) and Cape petrels (t_{31}=6.61, P<0.001). Mass-specific FMR did not differ between incubation stage in Cape and snow petrels (t_{12}=1.67, P=0.12), but was significantly higher during chick provisioning in snow petrels (t_{35}=2.01, P=0.049).

Adult water efflux rate during the chick provisioning stage was higher in snow petrels (805 ± 157 ml kg^{-1} d^{-1}) than Cape petrels (634 ± 107 ml kg^{-1} d^{-1}) (ANOVA; $F_{2,36}$=7.48, P=0.002). Comparisons with Antarctic petrels are inappropriate, given their small sample size (N=2).

Discussion

Nestling energy budgets

Antarctic fulmarine petrels exhibit a consistent pattern of nestling energy allocation (Fig. 5), despite differences in diet composition (Hodum, 1999) and body size. In all four species, TME increased until tissue accretion was maximal at 15–24 days of age – a period corresponding to the linear growth phase (Hodum, 1999). The rate of tissue deposition subsequently declined until net accretion ceased at 36–41 days of age. FMR increased until approximately the age at which net tissue deposition ceased, and then gradually declined until fledging. As a proportion of the total nestling energy budget, FMR varied from a low of 77% of TME in Antarctic petrels and fulmars to a high of 85% in snow petrels. Retained energy (RE=TME–FMR) comprised 15–22% of TME, ignoring losses due to mass recession (Fig. 5); the value was similar to the 13–28% value typical of birds generally (Roby, 1991; Weathers and Sullivan, 1991; Drent et al., 1992; Weathers, 1996). Drent et al. (1992) suggested that RE scales linearly with fledging mass and thus that the proportion of TME devoted to RE is relatively independent of body size. In Antarctic fulmarine petrels, the proportion of TME devoted to RE tended to increase with adult body size across species, although the four species differed by only 7%.

Time to fledging and fledging mass explain 97–99% of the variation in nestling TME and peak DME in 30 bird species, with increased growth rate simultaneously yielding an increased peak DME and a decreased TME (Weathers, 1992). Nestling periods of Antarctic fulmarine petrels are approximately half those predicted allometrically (Hodum, 1999), and thus one might expect TME values to be correspondingly reduced. Yet, measured TME values are 33–73% greater than predicted (Table 4). Higher than expected TME values in Antarctic fulmarine petrels, and arctic-nesting species with relatively short nestling periods (Weathers, 1992), may reflect relatively high thermoregulatory costs at high latitudes.

If, as suggested by Bryant and Hails (1983), it is the peak

Table 3. *Values of various parameters for adult Antarctic fulmarine petrels during the incubation and provisioning nestling stages of the breeding cycle*

Parameter	Cape petrel		Snow petrel		Antarctic petrel
	Incubation (N=7)	Nestling (N=26)	Incubation (N=7)	Nestling (N=11)	Nestling (N=2)
Recapture interval (days)	0.98±0.01	2.48±0.87	0.99±0.01	4.36±1.03	3.98±0.42
Body mass (g)	507±44	440±32	307±18	245±24	618±87
FMR (ml CO_2 g^{-1} h^{-1})	1.49±0.30	4.28±1.09	2.12±0.88	5.03±0.88	3.23±0.98
FMR[a] (kJ d^{-1})	481±101	1196±289	417±179	793±194	1302±569
FMR/BMR[b]	1.23±0.25	3.54±0.91	1.93±0.80	4.56±0.80	3.54±1.08
Water efflux (ml kg^{-1} d^{-1})	–[c]	634±107	–[c]	805±157	671±46
% mass change d^{-1}	–5.12±1.42	0.89±3.15	–6.74±2.80	–0.31±2.56	–0.42±0.17

Values are means ± S.D.

[a]FMR, field metabolic rate, calculated assuming 26.6 kJ l^{-1} CO_2 produced.

[b]BMR, basal metabolic rates, from Weathers et al. (2000).

[c]FMR of incubating adults was determined by the single-sample doubly labelled water method, which does not provide reliable estimates of water efflux (Webster and Weathers, 1989), hence none are provided.
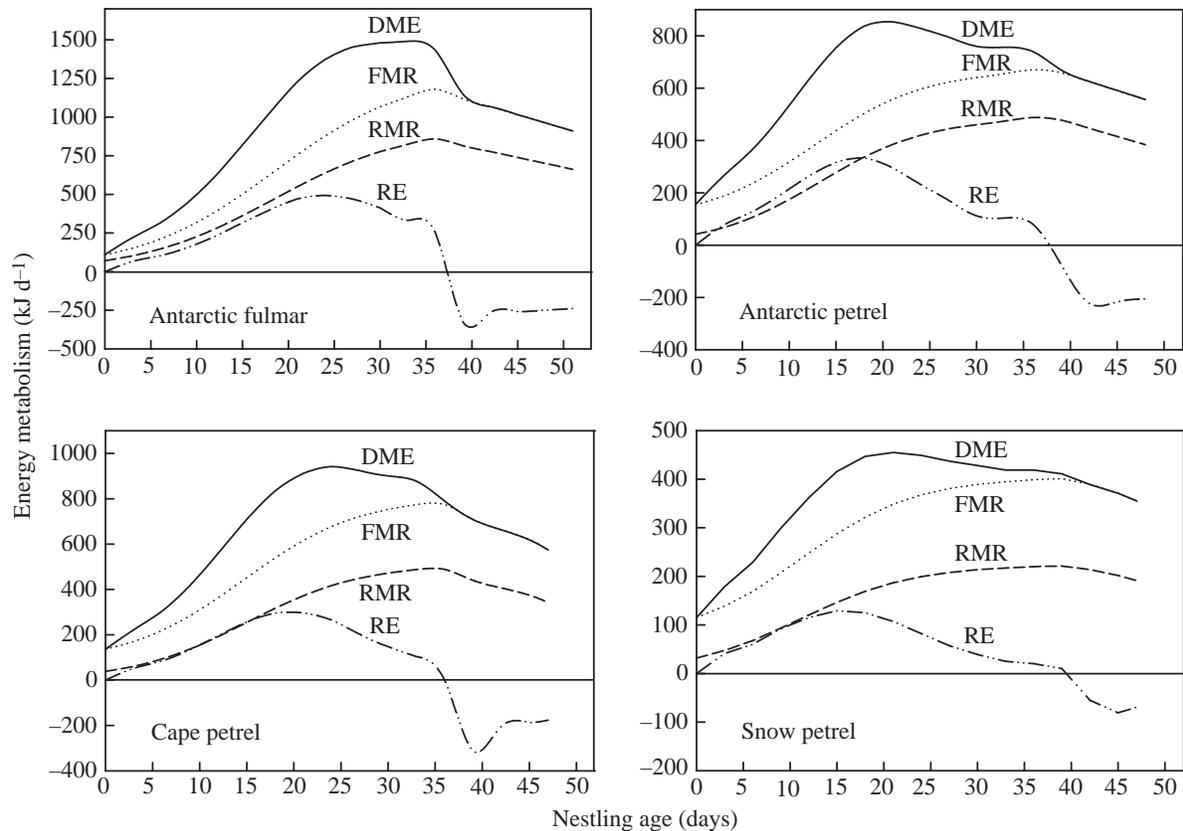
Fig. 5. Energy expenditure of nestling Antarctic fulmarine petrels as a function of age. DME, daily metabolized energy (FMR+RE); FMR, field metabolic rate; RMR, resting metabolic rate; RE, retained energy (energy accumulated in new tissue).

Table 4. *Observed peak daily metabolizable energy (DME) and total metabolizable energy (TME) of nestling Antarctic fulmarine petrels compared with values predicted allometrically*

Species	Fledging mass (g)	Time to fledging (days)	Peak DME (kJ d^{-1})			TME (kJ)		
			Observed	Predicted[a]	% of predicted	Observed	Predicted[b]	% of predicted
ANFU	808	52	1480	941	157	50692	32984	154
ANPE	590	48	854	732	117	31657	23838	133
CAPE	441	47	942	567	166	31728	18326	173
SNPE	246	47	455	334	136	17637	11145	158

[a]Predicted peak DME=$11.69M^{0.908} \times t_{fl}^{-0.428}$, where M = fledging mass and t_{fl} = time to fledging (Weathers, 1992).
[b]Predicted TME=$6.65M^{0.852} \times t_{fl}^{0.710}$, where M = fledging mass and t_{fl} = time to fledging (Weathers, 1992).
Species abbreviations as in Table 1.

energy demand of nestlings that limits reproduction rather than the total or average energy demand, one would expect interspecific variations in peak DME to correlate with life history traits in ways that are adaptive. For example, peak DME should be relatively low in species such as pelagic seabirds, whose parents have difficulty obtaining food due to a widely dispersed and unpredictable prey base (Lack, 1968; Ricklefs, 1983). Nestlings of the four species in this study had peak DME values ranging from 117% (Antarctic petrel) to

166% (Cape petrel) of the predicted values (Table 4). These relatively high DME values reflect the rapid growth rates of fulmarine petrels and the high costs of thermoregulation. Arctic species similarly have higher peak DME values than predicted (Weathers, 1996), a result that parallels the latitudinal gradient in hatchling metabolism (Klaassen and Drent, 1991). High TME and peak DME values suggest that obtaining sufficient food is generally not a constraint for adult fulmarine petrels, and that factors operating at the tissue level

may limit nestling growth rate in these species. In a study of diving petrels (*Pelecanoides* sp.) and least auklets (*Aethia pusilla*), Roby (1991) similarly concluded that growth was not limited by energy intake *per se*, but rather by tissue level constraints.

The relative cost of growth (R_c, TME/fledging mass) in Antarctic fulmarine petrels is among the highest reported for birds (for a summary, see Weathers, 1992), with Cape petrel (71.9 kJ g^{-1}) and snow petrel (71.7 kJ g^{-1}) nestlings being the most expensive to produce. These results confirm the suggestion by Simons and Whittow (1984) that petrels require considerably more energy per gram of fledgling than other species. Indeed, including our results, the five most 'expensive' fledglings to produce are all procellariiforms, and eight of the highest nine species are seabirds (Weathers, 1992; and this study). Presumably, increased thermoregulatory costs associated with a frigid environment partly accounts for the high R_c values of Antarctic fulmarine petrels. High R_c does not necessarily imply a constraint on breeding birds, however. Costly fledglings may not be disadvantageous when growth and energy requirements are dictated primarily by developmental rather than environmental controls.

Parental energy expenditure

Nagy and Obst (1991) noted that high-latitude seabirds that spend much time flying and/or have high wing loading have much higher FMR values than birds generally. They found FMR values of adults provisioning nestlings to be 200–220% of the predicted values in the least auklet, South Georgia diving petrel *Pelecanoides georgicus*, common diving petrel *P. urinatrix*, and the southern giant petrel *Macronectes giganteus*. Cape petrels and snow petrels provisioning nestlings similarly have FMR values that average 223% and 215% of the predicted values, respectively.

The relatively high FMR of Antarctic fulmarine petrels provisioning young mirrors the youngs' high energy requirement, but also reflects the adults' foraging mode, overall metabolic status and climate. Basal metabolic rates (BMR) of adult Antarctic fulmarine petrels average 40% higher than values predicted allometrically for nonpasserine birds (Weathers et al., 2000). A higher than predicted BMR, which is typical of seabirds in general and high-latitude species in particular (Ricklefs and Matthew, 1983; Ellis, 1984; Bennett and Harvey, 1987; Bryant and Furness, 1995), is apparently a consequence of an active lifestyle, rather than a primary adaptation to cold (Kersten and Piersma, 1987), and reflects the energy cost of tissues required to support high activity levels (Daan et al., 1990).

Adult FMR was independent of foraging trip duration, in contrast with the positive relationship between FMR and foraging trip duration shown by many seabirds (Gabrielsen et al., 1987, 1991, Birt-Friesen et al., 1989; Shaffer, 2000; but see Hodum et al., 1998). We lack data on foraging distances and at-sea activity, but if Antarctic fulmarine petrels spend most of their time during a foraging trip in flight, then their rate of energy expenditure would remain uniform on a daily basis. A uniform daily rate of energy expenditure would yield an FMR that is independent of foraging trip duration.

In addition to a high FMR, adults of all three measured species had higher water efflux rates than predicted allometrically. Rates were 2.8 (Cape petrel), 3.1 (snow petrel) and 3.3 (Antarctic petrel) times those predicted for mostly aquatic birds with salt glands (Hughes et al., 1987) and 4.3–5.2 times those predicted for seabirds (Nagy and Peterson, 1988). Similarly high rates of water efflux were found in Cassin's auklets *Ptychoramphus aleuticus*, another pelagic seabird (Hodum et al., 1998), and tufted ducks *Aythya fuligula* (de Leeuw, 1997). Petrels, like auklets and tufted ducks, capture prey at sea and thus presumably ingest water that is attached to prey items. The high water content of these prey items may also contribute to high water turnover rates.

Physiological work rates of parent birds can be expressed as the ratio FMR/BMR (Drent and Daan, 1980), a high ratio implying a high level of parental effort. Drent and Daan (1980) suggested that parent birds work to their physiological capacity when rearing young and that the FMR/BMR ratio converges on a value of 4, which denotes maximum sustainable effort. This ratio was subsequently revised upwards to 5–5.7 by Weathers and Sullivan (1989), who noted that relatively few species appeared to work maximally when rearing young. Indeed, FMR/BMR ratios of breeding birds range widely from 1.3–6.7 (Masman et al., 1989; Weathers and Sullivan, 1989; Peterson et al., 1990). In seven species of high latitude (>45°) procellariiform birds other than albatrosses, mean FMR/BMR=4.0±0.5 (Ellis and Gabrielsen, 2001), signifying a relatively high level of parental effort.

In both Cape and snow petrels, FMR/BMR was lower during the incubation stage, when adults were on the nest, than during the nestling stage, when they were foraging at sea (Table 3). Parental effort during the nestling period was identical in adult Cape and Antarctic petrels (3.5 times BMR), and was somewhat (but not significantly) higher in snow petrels (4.6 times BMR). These ratios are typical of other high-latitude procellariids. Thus, despite the constraints of a compressed breeding season and nestlings that grow 150–200% faster than predicted, breeding Antarctic fulmarine petrels do not appear to work harder than procellariids whose chicks grow much more slowly. Presumably food is so abundant near Hop Island that adults can provision their rapidly growing chicks without additional effort.

List of symbols and abbreviations

BMR	basal metabolic rate
DLW	doubly labeled water technique
DME	daily metabolizable energy
EC	energy content
FMR	field metabolic rate
M	adult mass
m	wet mass
ME	metabolizable energy
R_c	relative cost of growth

RE   retained energy
RMR   resting metabolic rate
TBW   total body water
TME   total metabolizable energy
WE   water efflux
W_f fraction of mass consisting of water

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