



## FIELD ENERGY EXPENDITURES OF THE SOUTHERN GIANT-PETREL<sup>1</sup>

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**Abstract.** We used the doubly labeled water method to measure rates of energy expenditure in free-living Southern Giant-Petrels (*Macronectes giganteus*, mean body mass = 3.89 kg) at Palmer Station, Antarctica. Despite superficial morphological and behavioral resemblances to the energetically efficient albatrosses, giant-petrels have high energetic costs while foraging, averaging  $6.3 \times$  SMR (standard metabolic rate), which is much higher than the values for three *Diomedea* albatrosses ( $1.8$  to  $2.7 \times$  SMR). The integrated field metabolic rate (FMR, incorporating time spent foraging and brooding) of a giant-petrel is  $4,270 \pm 668$  kJ day<sup>-1</sup>, the highest absolute value yet measured in any bird. Their overall FMR is  $4.6 \times$  SMR, slightly higher than the suggested upper limit of  $4.0 \times$  SMR for breeding birds. Compared with similar-sized albatrosses, Southern Giant-Petrels are more heavily wing-loaded, they flap more frequently, and they deliver meals more frequently to their chicks. These factors probably contribute to their higher rates of energy expenditure. Giant-petrels breed most abundantly at high latitudes, outside the breeding range of albatrosses. An energy-expensive breeding strategy that incorporates relatively rapid nestling growth and high rates of chick-feeding by adults may account for the success of Southern Giant-Petrels in the short growing season Antarctic habitat.

**Key words:** *Breeding costs; convergent evolution; doubly labeled water; field metabolic rate; flight morphology; foraging costs.*

### INTRODUCTION

The avian community of the southern oceans contains mainly large species, including the pursuit-diving penguins (Spheniscidae) and the long-winged, soaring albatrosses (Diomedidae). Members of these two families account for the vast majority of the avian biomass of the antarctic and subantarctic regions (Croxall et al. 1984a, Hunt 1985). Owing to their importance as pelagic predators in the southern oceans, considerable attention has been devoted to measurements of the energy expenditures of these birds. Recent studies have indicated that albatrosses have among the most economical of foraging costs among those birds studied to date,

with field metabolic rates (FMRs) while at sea being as low as  $1.8 \times$  SMR (standard metabolic rate, Adams et al. 1986). These low rates of energy expenditure have been attributed to the morphological adaptations possessed by these birds that permit them to utilize the wind energy for propulsion via "dynamic soaring" in the open ocean habitat.

Giant-petrels (*Macronectes* spp.) comprise an evolutionarily distinct group of large seabirds that is confined to waters of the Southern Hemisphere. Although they are less abundant than the albatrosses, they exhibit some striking convergences with the Diomedidae, particularly with respect to their general size, shape and dynamic-soaring habits. Giant-petrels are a conspicuous part of the southern avifauna, breeding from the subantarctic area, where albatrosses also breed, south to coastal Antarctica and the Antarctic

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Peninsula, where albatrosses do not breed. In the present study, we used the doubly labeled water method (Lifson and McClintock 1966, Nagy 1980) to determine whether the apparent morphological convergence between the albatrosses and the Southern Giant-Petrel (*Macronectes giganteus*) would result in similarly economical energy expenditures for this antarctic breeder.

## METHODS

### STUDY SITE

Field work was conducted on Humble Island, an islet about 1.5 km west of Palmer Station, Antarctica (64.44°S, 64.03°W), between 15 and 22 January 1984. About 75 pairs of Southern Giant-Petrels were nesting on Humble Island in loose, scattered groups. During our study, extreme air temperatures, recorded by a maximum-minimum thermometer placed in continuous shade on the island, were  $-2.0$  and  $+6.2^{\circ}\text{C}$ . Mean daily shaded air temperature recorded at a meteorological station at Palmer Station was  $+1.1^{\circ}\text{C}$ , and wind velocity averaged  $6\text{ m}\cdot\text{sec}^{-1}$  (range 0 to  $20\text{ m}\cdot\text{sec}^{-1}$ ).

### FIELD PROCEDURES

Eight nests containing small chicks (brood stage) were selected for study. At each nest, the brooding adult was restrained by grasping its bill and holding it while it continued to sit on the nest. Then, it was marked for subsequent identification by spraying paint lightly on the upper breast and neck. After one day, the nests were checked for the presence or absence of marked adults. In all eight cases, a nest-exchange had occurred and the unmarked mate was brooding the chick.

Each of these unmarked adults was captured and placed in a burlap (Hessian) bag. The chick was immediately covered with another bag to keep it warm and quiet, and to protect it from Skua predation. Each adult giant-petrel was weighed to the nearest 0.25 kg with a 10 kg Pesola spring scale, and given an intramuscular (pectoral muscle) injection of 1.386 ml of doubly labeled water ( $^3\text{H}^1^8\text{O}$ ). Isotope enrichments in the injection solution were  $1.50\text{ mCi}\cdot\text{ml}^{-1}$  for  $^3\text{H}$  and 92 atoms percent for  $^{18}\text{O}$ . The birds were individually marked with paint and released back onto their nests within a few minutes of capture. The isotopically labeled water was allowed to equilibrate with the birds' body water while they sat on the nest for 2.5 hr. Then, each bird was again captured, and a 7-ml blood sample was

removed from a leg or wing vein. Finally, the birds were released again at their nests, where they resumed brooding immediately. Marked birds showed no evidence of residual disturbance from our handling. Blood samples were taken from two uninjected giant-petrels for measurement of natural abundances of the two isotopes.

The study nests were checked 3–4 times per day at irregular intervals over the five days following the injections. The presence or absence of each of the individually-marked mates was recorded. Within 24 hr of injection, another nest exchange had taken place at each of the eight nests, with the injected bird having left to forage and the non-injected mate remaining to brood the chick. At the first nest check at which an injected bird was found to have returned from foraging, it was recaptured, reweighed, and a second blood sample was taken. The bird was then released at the nest to complete another cycle of brooding and foraging. In five individuals, a third sample was taken after they had returned from a second foraging trip. Thus, we were able to obtain estimates of the FMRs of eight birds during a total of 13 cycles of brooding and foraging.

### TIME BUDGETS

The length of the 13 measurement periods varied considerably, as did the proportions of time spent on and off the nest. We were never present at a nest at the exact moment that an injected bird left for, or returned from, the sea. Consequently, we estimated the percentage of each measurement period spent on the nest (brooding) and off the nest (presumably foraging) by assuming that each nest exchange occurred midway between the time the nest was checked prior to, and again after, a change in brooding duty was recorded. We calculate that the *maximum* error associated with these estimates (i.e., the error that would occur if all nest exchanges took place immediately before or after our nest checks, rather than midway between them) would average 15.0% ( $SE = 1.5$ ,  $n = 13$ ) of the total measurement period.

One injected adult was confined to its nest while brooding, by placing a large ( $1.5 \times 1.5 \times 2.0\text{ m}$ ) wire-mesh cage over the nest and bird. This cage prevented its non-injected mate from approaching the brooding bird and initiating a successful nest exchange. The cage did not appear to otherwise interfere with the brooding bird's normal nest behavior; we witnessed no evidence of the bird trying to escape from or otherwise

manipulate the cage. Using this method, we were able to keep the bird sitting on the nest for two days, a period exceeding the species' typical brooding spell, but long enough to allow for sufficient isotope turnover for the estimation of FMR during brooding.

#### DETERMINATION OF SEX

Southern Giant-Petrels are sexually dimorphic, with no overlap occurring in bill length but some overlap in body mass (Conroy 1972, Hunter 1984). We used these two characters in combination to determine the sexes of the injected and non-injected members of each of the eight study pairs. Birds with body masses  $>4.0$  kg and culmen length  $>95$  mm were considered to be males, while individuals whose measurements fell below these threshold values were considered to be females. Within each pair, there was only one male-sized individual and one female-sized individual, by these criteria.

#### SAMPLE ANALYSIS AND CALCULATIONS

Blood samples were microdistilled to complete dryness to obtain pure water devoid of isotopic fractionation errors. The water was then analyzed for tritium by liquid scintillation counting, and for oxygen-18 by proton activation analysis (Wood et al. 1975, Nagy 1983). The oxygen-18 levels in blood samples from birds recaptured a second time had become too low (below about 0.23 atoms percent) to yield reliable results from activation analysis, so these samples were analyzed by isotope ratio mass spectrometry at Global Geochemistry Corporation (Canoga Park, California). Mass spectrometric measurements are accurate to very low enrichments of oxygen-18, and this technique yields reliable FMR measurements (Schoeller and van Santen 1982, Schoeller and Webb 1984). Rates of  $\text{CO}_2$  production and water flux were calculated using the equations for linearly-changing body water volumes (Nagy 1980, Nagy and Costa 1980), and heat equivalents of  $\text{CO}_2$  volumes were calculated assuming a diet of fish yields  $25.8 \text{ kJ (liter } \text{CO}_2)^{-1}$  (Nagy et al. 1984).

Statistical methods for comparisons of sample means, simple linear regression, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) follow Sokol and Rohlf (1981). Values below are expressed as mean  $\pm$  95% confidence interval of the mean, unless otherwise stated. The 95% CI values reported for the intercepts of

regression lines were calculated from the equations for the 95% CI envelope for the least squares lines.

## RESULTS

### TIME BUDGETS

The length of 13 brooding spells by the eight injected birds ranged from 5 hr to 45 hr, averaging  $24.0 \pm 7.1$  hr. Foraging bouts lasted between 9 hr and 37 hr, and averaged  $24.8 \pm 4.4$  hr. There was no significant difference between the sexes in either the length of brooding spells or foraging trips ( $P > 0.75$ ). Furthermore, the mean lengths of brooding and foraging bouts were also statistically indistinguishable ( $P > 0.35$ ), suggesting that on average, both mates divide their time equally between brooding spells and foraging trips, with nest exchanges occurring about once per day.

In order to determine whether repeated handling of the giant-petrels affected their time budgets, we paint-marked pairs at seven additional nests without capturing them, and monitored their patterns of nest attendance from afar. These birds were disturbed only once, by grasping and holding their bills for a few seconds while spray-painting their neck, at the beginning of the five-day observation period. There were no significant differences in the lengths of brooding or foraging bouts between the two groups, whether the data for the two sexes were analyzed separately, or were pooled (ANOVA,  $P > 0.75$ ).

### BODY MASS, WATER FLUX

Among the eight injected birds, three were males and five were females. Males were significantly larger, with a mean body mass of  $4.55 \pm 0.32$  kg, while females averaged  $3.57 \pm 0.21$  kg. Changes in body mass during the measurement periods ranged from  $-3.8$  to  $+9.1\%$  per day (Table 1). The rate of change in body mass was significantly correlated with the percentage of the measurement period spent away from the nest ( $r = 0.55$ ,  $P < 0.05$ ). The (extrapolated) intercepts at zero percent time and 100 percent time away from the nest suggest that on average, giant-petrels lose about 5% ( $4.6 \pm 0.7\%$ ) of their body mass per day while on the nest, and gain 5% ( $5.0 \pm 0.6\%$ ) per day while away foraging.

Total body water of the eight individuals at first capture, as determined from the  $^{18}\text{O}$  dilution space, averaged  $51.7 \pm 1.6$  percent of total body

TABLE 1. Field metabolic rates (FMRs) and water influx rates (WIRs) of Southern Giant-Petrels nesting near Palmer Station, Antarctic Peninsula.

Anim. # (sex)	Meas. period, days	% of period off nest	Body mass		FMR		WIR, ml·kg <sup>-1</sup> ·day <sup>-1</sup>
			Mean, g	Change, %/day	ml CO <sub>2</sub> ·g <sup>-1</sup> ·hr <sup>-1</sup>	kJ·day <sup>-1</sup>	
1 (F)	2.1	68	3,475	3.4	1.26	2,710	242
	2.1	64	3,575	-0.7	2.89	6,400	117
2 (M)	1.1	79	4,475	9.1	2.08	5,760	173
	2.0	45	4,725	0.5	1.92 <sup>a</sup>	5,620	98
3 (F)	2.4	33	3,525	-1.5	1.57	3,430	91
	1.4	82	3,400	-2.2	2.68 <sup>a</sup>	5,640	98
4 (M)	2.8	54	4,650	-0.8	1.38	3,970	131
	1.3	84	3,575	-1.1	1.85	4,100	162
5 (F)	1.8	42	3,500	-1.6	1.82 <sup>a</sup>	3,940	108
	2.8	49	3,475	-0.5	1.62	3,490	172
7 (F)	1.7	22	3,975	-2.2	0.95	2,340	85
	2.1	32	3,750	-3.8	2.18 <sup>a</sup>	5,060	107
8 (M)	2.0	29	4,400	-3.4	1.40	3,810	118
Mean	2.0	53	3,885	-0.4	1.82	4,330	131
SD	0.5	21	498	3.4	0.55	1,260	45

<sup>a</sup> These rates of CO<sub>2</sub> production were calculated using mass spectrometer measurements of <sup>18</sup>O in blood samples, rather than proton activation measurements, as used in obtaining the other results.

mass, with no differences between the sexes ( $P > 0.50$ ). Rates of water influx ( $W_{in}$ , in units of ml·kg<sup>-1</sup>·day<sup>-1</sup>) were positively correlated with the percent time spent away from the nest ( $W_{in}$

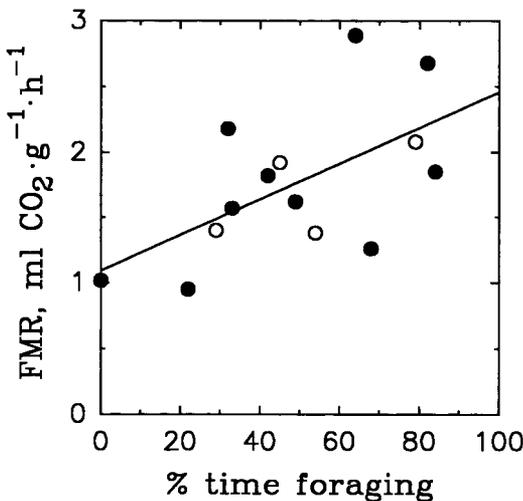


FIGURE 1. Field metabolic rate (FMR) of Southern Giant-Petrels (*Macronectes giganteus*) at Palmer Station, Antarctic Peninsula increased as the proportion of the measurement interval spent away from the nest (foraging) increased. Closed circles represent males and open circles represent females. The solid line represents the least-squares regression line for both sexes combined [ml CO<sub>2</sub>·g<sup>-1</sup>·hr<sup>-1</sup> = 1.091 + 0.0137(% time foraging),  $r = 0.59$ ,  $P < 0.05$ ].

= 19 + 2.62 [% time away];  $r = 0.64$ ,  $P < 0.05$ ). Inspection of the intercepts of this regression suggest that the average water input rate while on the nest (essentially all due to metabolic water production) was 19 ml·kg<sup>-1</sup>·day<sup>-1</sup>, and water influx during foraging trips was 281 ml·kg<sup>-1</sup>·day<sup>-1</sup>. Water influx rate was significantly ( $F_{(1, 11)} = 6.52$ ,  $P < 0.05$ ) correlated with rate of body mass change, and the intercept of the regression equation indicated that a giant-petrel maintaining constant body mass would have a water influx rate of  $134 \pm 23$  ml·kg<sup>-1</sup>·day<sup>-1</sup>.

#### FIELD METABOLIC RATES

FMRs, measured as rates of CO<sub>2</sub> production during the 13 measurement periods, ranged from 1.26 to 2.89 ml CO<sub>2</sub>·g<sup>-1</sup>·hr<sup>-1</sup>, equivalent to a range of 2,710–6,400 kJ·day<sup>-1</sup> (Table 1). As with water influx, there was a strong, positive correlation between FMR and the percentage of the measurement period spent away from the nest (Fig. 1). The  $y$ -intercept (time away = 0) suggests that FMR during brooding averages  $1.092 \pm 0.571$  ml CO<sub>2</sub>·g<sup>-1</sup>·hr<sup>-1</sup> ( $2,624 \pm 1,372$  kJ·day<sup>-1</sup>). (The single value we obtained for brooding FMR from the caged bird [1.018 ml·g<sup>-1</sup>·hr<sup>-1</sup>, or 2,446 kJ·day<sup>-1</sup>] is included in the regression in Fig. 1.) For foraging birds (percent time away = 100), FMR was estimated to average  $2.462 \pm 0.646$  ml CO<sub>2</sub>·g<sup>-1</sup>·hr<sup>-1</sup>, or  $5,915 \pm 1,552$  kJ·day<sup>-1</sup>. Birds

spending 50% of their time on and 50% of their time off the nest would have an integrated FMR averaging  $1.777 \pm 0.278 \text{ ml CO}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$  or  $4,270 \pm 668 \text{ kJ} \cdot \text{day}^{-1}$ .

Because males were 27% larger than females, one might expect rates of (whole animal) energy expenditure to differ between sexes. After accounting for the slight difference between sexes in time budgets (see Fig. 1), there was still a tendency for males to have higher  $\text{kJ} \cdot \text{day}^{-1}$  values, but the difference was not significant (ANCOVA,  $P > 0.35$ ). Therefore, values for the two sexes are pooled in subsequent analyses.

To facilitate comparisons between species, it is useful to express FMR as a multiple of standard metabolic rate (SMR). Published values for SMR of Southern Giant-Petrels are  $1,628 \text{ kJ} \cdot \text{day}^{-1}$  (Ricklefs and Matthew 1983) and  $937 \text{ kJ} \cdot \text{day}^{-1}$  (Bennett and Harvey 1987), as recalculated for a 3,880-g bird (assuming  $\text{RQ} = 0.73$  and  $27.75 \text{ kJ} \cdot \text{liter CO}_2^{-1}$  for lipid metabolism). An unpublished value for SMR is  $1,110 \text{ kJ} \cdot \text{day}^{-1}$  (K. Morgan, M. Chappell, and T. Bucher, pers. comm.). Using the lowest of these SMR values, we calculated FMR multiples of  $2.80 \pm 1.49 \times \text{SMR}$  during brooding,  $6.31 \pm 2.24 \times \text{SMR}$  during foraging, and  $4.56 \pm 0.71 \times \text{SMR}$  overall.

## DISCUSSION

### TIME BUDGETS

During the brood stage, adult Southern Giant-Petrels at Palmer Station divide their time equally between brooding and foraging trips. This agrees with data gathered on the same species at South Georgia (Hunter 1984), and appears to be a pattern typical of procellariiform birds in general. However, Hunter (1984) found that at South Georgia, chicks were fed two times a day, implying that adult foraging trips lasted only 12 hr on average. Foraging trips by the birds we studied lasted twice that long (24 hr).

Hunter (1984) characterized Southern Giant-Petrels at South Georgia as being scavengers, depending heavily upon carcasses of penguins and fur seals for food. Penguins are abundant breeders on South Georgia where the ratio of breeding penguins to breeding giant-petrels is about 1,100:1 (Croxaal et al. 1984b). Breeding penguins are far less numerous near Palmer Station. On the nearby South Shetlands, where bird colonies have been particularly well-censused, the ratio of penguins to giant-petrels is 75:1, more than an order

of magnitude lower than at South Georgia. Furthermore, no concentrations of summer-breeding seals exist in the vicinity of Palmer Station. It is therefore likely that giant-petrels at Palmer have a different diet, and must range farther in search of food than do those at South Georgia. This would help to explain the longer foraging trips by the birds at Palmer. In support of this suggestion are satellite-tracking experiments with Southern Giant-Petrels nesting on Humble Island, which indicate that males may travel as far as 250 km away from the colony on a single foraging trip (Strikwerda et al. 1986). Although there are no quantitative dietary data for giant-petrels breeding in the Palmer area, our qualitative impression from inspection of the food regurgitated by adults and chicks during handling is that marine invertebrates, especially krill and squid, comprise a larger fraction of a diet at Palmer than they do in the diets of birds in colonies farther to the north (Hunter 1983).

### RATES OF ENERGY EXPENDITURE

Field metabolic rates of free-living Southern Giant-Petrels were remarkably high. The integrated FMR of  $4,330 \text{ kJ} \cdot \text{day}^{-1}$  is 206% of the value predicted by eq. 5.75 of Kendeigh et al. (1977) for breeding non-passerine birds at  $0^\circ\text{C}$ , 220% of the value predicted by eq. 8 of Walsberg (1983) for free-living birds, and 160% of the FMR value predicted for a 3,880-g bird by eq. 36 of Nagy (1987) for seabirds. In fact, this FMR is the highest value yet measured in any bird species, including the larger Wandering Albatross (*Diomedea exulans*, Table 2, Nagy 1987, Nagy and Obst 1991).

Drent and Daan (1980) proposed that  $4.0 \times \text{SMR}$  may be "a maximum sustained working level for all parent birds." Southern Giant-Petrels apparently exceeded this limit slightly during our study, having an integrated FMR (brooding and foraging) that was  $4.56 \times \text{SMR}$ . However, this comparison is very sensitive to the SMR measurements used in calculating the ratio of FMR:SMR. Several other species of seabird also apparently exceed this limit: Wedge-tailed Shearwater, *Puffinus pacificus*,  $4.3 \times \text{SMR}$ ; Northern Gannet, *Sula bassanus*,  $6.7 \times \text{SMR}$ ; Macaroni Penguin, *Eudyptes chrysolophus*,  $5.8 \times \text{SMR}$  (summarized by Peterson et al. 1990). Many species of birds other than seabirds also exceed the  $4.0 \times \text{SMR}$  level (Bryant 1991, Bryant and Tatner 1991), as do some species of eutheri-

TABLE 2. Comparison of rates of energy expenditure during foraging by three albatross species (*Diomedea* spp.) and the Southern Giant-Petrel (*Macronectes giganteus*).

Species	Metabolic rate while foraging			Source of data
	ml CO <sub>2</sub> ·g <sup>-1</sup> ·hr <sup>-1</sup>	kJ·day <sup>-1</sup>	× SMR	
Wandering Albatross	0.656	3,354	1.83	Adams et al. 1986
Grey-headed Albatross	1.074	2,402	2.50	Costa and Prince 1987
Laysan Albatross	1.141	2,072	2.66	Pettit et al. 1988
Albatross mean	0.957	2,609	2.33	
SD	0.263	666	0.44	
Southern Giant-Petrel	2.462	5,915	6.31	This study
Significance level of difference*	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> < 0.05	

\* Two-tailed t-test for comparison of a single observation (Southern Giant-Petrel) with a mean of a sample (albatrosses) after Sokal and Rohlf (1981). *P* is the probability that the giant-petrel value belongs to the statistical population comprised by the albatrosses.

an and marsupial mammals (Peterson et al. 1990). However, animals with high FMRs tend to have high SMRs as well (Daan et al. 1991, Koteja 1991), so evaluating the intensity of FMR only as a multiple of SMR may mask important differences between species in their absolute capacity for sustained work.

#### WATER FLUX

Metabolic water production during brooding averaged 19 ml·kg<sup>-1</sup>·day<sup>-1</sup>, or about 74 ml·bird<sup>-1</sup>·day<sup>-1</sup> for a bird of mean mass of 3.88 kg. The ratio of water production to FMR at the nest was 0.028 ml·kJ<sup>-1</sup> [(74 ml·day<sup>-1</sup>) / (2,624 kJ·day<sup>-1</sup>)]. This value is very close to the value of 0.027 ml·kJ<sup>-1</sup> for the metabolism of pure lipid (Nagy and Peterson 1988). For a bird that is maintaining steady-state energy and mass budgets, we estimated (above) that water influx would be 134 ml·kg<sup>-1</sup>·day<sup>-1</sup>, or 520 ml·bird<sup>-1</sup>·day<sup>-1</sup>. Using an integrated FMR of 4,270 kJ·day<sup>-1</sup>, we calculated the water economy index (WEI, Nagy and Peterson 1988), which is the ratio of water intake to energy metabolism, to be 0.12 ml H<sub>2</sub>O·kJ<sup>-1</sup>. This value is about in the middle of the range of ratios expected for carnivorous animals that do not drink free water (0.08 to 0.18, Nagy and Peterson 1988), which suggests that Southern Giant-Petrels also did not drink sea water or snow-melt water during our measurements.

#### IMPACT UPON PREY RESOURCES

Hunter (1985) estimated the global impact of giant-petrels on prey resources, based upon published estimates of the world-wide population, data on diet, and a model for estimating the energy requirements of free-living seabirds pro-

posed by Croxall and Prince (1982). This model uses multiples of the predicted existence energy requirement (EER; Kendeigh et al. 1977) to estimate the energetic costs of various activities, e.g., 1.0 × EER for brooding and 1.85 × EER for foraging. Assuming that the energetic costs of sitting at the nest and foraging remain constant throughout the breeding cycle, we can calculate the energy requirements of Southern Giant-Petrels during the breeding season from our measurements of FMR, for comparison with Hunter's estimates.

The breeding cycle of the Southern Giant-Petrel lasts ca. 178 days, with 41 days spent on the nest incubating and brooding, and 137 days spent foraging by each adult (Hunter 1985). Multiplying these values by our estimates of FMR during brooding and foraging yields:

$$\begin{aligned}
 & (41 \text{ days}) \cdot (2,624 \text{ kJ} \cdot \text{day}^{-1}) \\
 & + (137 \text{ days}) \cdot (5,915 \text{ kJ} \cdot \text{day}^{-1}) \\
 & = 9.18 \cdot 10^5 \text{ kJ} \cdot \text{season}^{-1}, \\
 & \text{or } 1.84 \cdot 10^9 \text{ J} \cdot \text{pair}^{-1} \cdot \text{season}^{-1}.
 \end{aligned}$$

This value is nearly triple Hunter's estimate of 0.62 · 10<sup>9</sup> J·pair<sup>-1</sup>·season<sup>-1</sup> for Southern Giant-Petrels breeding in the Antarctic Peninsula region. Even if our higher estimate were only applicable to the Antarctic Peninsula population, comprising an estimated 44% of the world's Southern Giant-Petrels, the global energy requirements for breeding pairs would be 4.35 · 10<sup>13</sup> J·season, almost double Hunter's global estimate.

Hunter (1985) estimated that 75% of the energy requirements of Antarctic Peninsula giant-petrels are met by eating penguin carcasses. This

TABLE 3. A comparison of aspects of the flight morphology of albatrosses (Diomedidae) with the Southern Giant-Petrel (*Macronectes giganteus*).<sup>a</sup>

	Aspect ratio	Wing loading, N·m <sup>-2</sup>	Wing disc loading, N·m <sup>-2</sup>
Albatrosses: mean	15.0	119.4	10.0
(SD, n)	(0.5, 6)	(28.8, 9)	(2.3, 6)
Southern Giant-Petrel	11.9	163.0	15.0
Significance level of difference <sup>b</sup>	$P < 0.01$	$0.1 < P < 0.2$	$P < 0.05$

<sup>a</sup> Values used in this comparison are from Table 1 in Warham (1977). Wing disc loadings (DL) were calculated as  $DL = W[-(S/2)]^{-1}$ , where  $W$  is body weight and  $S$  is wing span.

<sup>b</sup> Two-tailed t-test for comparison of a single observation (Southern Giant-Petrel) with the mean of a sample (albatrosses) after Sokol and Rohlf (1981).  $P$  is the probability that the giant-petrel value belongs to the statistical population comprised by the albatrosses.

would require the local consumption of  $4.5 \cdot 10^6$  penguins per summer, equivalent to 30% of all penguins known to breed in the region (Croxall et al. 1984a). This is highly unlikely, and supports our preliminary impression that diets of Antarctic Peninsula and South Georgia Southern Giant-Petrels differ.

#### COMPARISON WITH ALBATROSSES

Field metabolic rates have been measured in three species of albatross: Wandering Albatross (*Diomedea exulans*; Adams et al. 1986); Grey-headed Albatross (*D. chrysostoma*; Costa and Prince 1987); and Laysan Albatross (*D. immutabilis*; Pettit et al. 1988). Estimates of FMR during foraging are low for all three species, averaging  $2.33 \times \text{SMR}$  (range 1.83 to 2.66; Table 2), compared with the high value for the Southern Giant-Petrel ( $6.31 \times \text{SMR}$ ). Economical foraging in albatrosses has been attributed to their ability to use wind energy for propulsion while soaring (Pennycuik 1982, Pennycuik et al. 1984), an ability seemingly shared by the giant-petrels. What then might account for the markedly higher foraging costs we measured in the Southern Giant-Petrel?

While giant-petrels are qualitatively similar to albatrosses in size, shape, and style of flight, they differ in important ways. On the wing, giant-petrels give the impression of being more heavy and clumsy in comparison with the buoyant gracefulness of the albatrosses. The quantitative basis of this difference is apparent from the data of Pennycuik (1982), who measured various aspects of the morphology and flight performance of Southern Hemisphere procellariiforms. Compared with albatrosses, giant-petrels have wings with lower aspect ratios (= wing span/wing width), a higher wing loading (= body weight/wing surface area), and a much higher wing-disc loading (= body weight/wing disc area; Table 3). Thus, the key morphological adaptations for dynamic

soaring are substantially less developed in giant-petrels. Giant-petrels are the largest members of the family Procellariidae, exceeding the next largest petrels by around 3 kg in body mass. Despite this fact, the species' wing proportions are generally well-predicted by a series of allometric regressions relating wing morphology to body mass among the smaller procellariids (Table 4). In contrast, corresponding allometric equations generated using data for albatrosses predict a flight morphology for a 4,500-g bird that differs substantially from that of the 4,500-g giant-petrel (Table 4). In short, giant-petrels can be considered to be simply "scaled-up" procellariids in general, and fulmars in particular. Thus, phylogenetic constraints may play a major role in determining the giant-petrel's proportions, perhaps posing limits to the seeming convergence between giant-petrels and albatrosses.

As a consequence of these morphometric differences, giant-petrels spend a much higher proportion of their time at sea engaged in flapping flight than do albatrosses. Pennycuik (1982) reported that the incidence of flapping flight while flying over the open ocean was only 7% and 6% for Wandering Albatrosses and Grey-Headed Albatrosses, respectively. The use of flapping flight by these albatrosses at sea is essentially limited to windspeeds below  $1 \text{ m} \cdot \text{sec}^{-1}$ . In contrast, giant-petrels employ flapping flight a substantial portion of the time at windspeeds up to  $8 \text{ m} \cdot \text{sec}^{-1}$  (Fig. 7 in Pennycuik 1982); the species' incidence of flapping flight was 24% or 3.5–4.0 times the albatross values. Owing to their high wing-disc-loading (the highest value calculated from data for 35 procellariiform species listed in Warham 1977), we can predict that flapping flight is relatively expensive for giant-petrels, and its frequent use would tend to increase energy expenditures during foraging.

Other factors may contribute to the high FMR

TABLE 4. A comparison of aspects of flight morphology of the Southern Giant-Petrel with allometric predictions for an albatross or a procellariid petrel of the same body mass ( $W = 4,500$  g). The least-squares regression equations shown were generated from data in Warham (1977).

	Wingspan, cm	Wing area, cm <sup>2</sup>	Wing loading, N·m <sup>-2</sup>	Aspect ratio
Southern Giant-Petrel				
Measured (actual) value	195	2,748	163	11.9
Albatrosses (Diomedidae)				
Allometric eqn. (Corr. coeff., $n$ )	$19.8W^{0.294}$ (0.98, 6)	$43.4W^{0.519}$ (0.91, 9)	$24.0W^{0.199}$ (0.80, 9)	$12.9W^{0.017}$ (0.23, 6)
Value predicted for $W = 4,500$ g	235	3,414	128	15.0
Actual/predicted	0.83	0.80	1.27	0.79
Petrels (Procellariidae) <sup>a</sup>				
Allometric eqn. (Corr. coeff., $n$ )	$9.77W^{0.366}$ (0.95, 23)	$20.1W^{0.583}$ (0.94, 28)	$4.91W^{0.416}$ (0.88, 28)	$4.98W^{0.125}$ (0.72, 23)
Value predicted for $W = 4,500$ g	212	2,716	163	14.2
Actual/predicted	0.92	1.01	1.00	0.84

<sup>a</sup> Values for the two giant-petrel species were not included in the derivations of the petrel regression equations.

as well. In a comparison of the energy expenditures of adult and nestling Wilson's and Leach's Storm-Petrels, Obst (unpubl.) suggested that the need for higher chick-feeding rates may have selected for a more energy-intensive foraging strategy in Wilson's Storm-Petrel, involving more time spent in flight and higher flight speeds. Southern Giant-Petrels deliver food to their chicks an average of two to six times more frequently than do Southern Hemisphere albatrosses (Pennycuik 1982). Costs associated with obtaining and transporting these frequent loads may increase giant-petrel energy expenditures above those of albatrosses.

#### EVOLUTIONARY CONSIDERATIONS: CONVERGENCE AND COMPETITION

Although giant-petrels and albatrosses are both widely distributed in high-latitude seas of the Southern Hemisphere, Southern Giant-Petrels reach their greatest abundance as breeders on the coast of the Antarctic Peninsula and its adjacent islands (Croxall et al. 1984a). This region is outside the breeding range of any albatross. The success of the petrels at high latitudes is attributable in part to their relatively rapid growth, a trait shared by all of the fulmarine petrels. Because giant-petrel nestlings complete their development in only 115 days compared to 141–281 days for albatrosses, Southern Giant-Petrels can complete their breeding cycle in under six months, and thereby avoid extremes of the early

antarctic winter. At subantarctic latitudes where albatrosses breed most successfully, giant-petrels breed in smaller numbers and appear to emphasize scavenging and land-based predation over pelagic foraging. We speculate that the higher energetic costs of foraging by giant-petrels would make them poor competitors with albatrosses, but that high rates of growth and provisioning allow them to breed successfully at latitudes where the reproductive season is too short for albatrosses to complete their breeding cycles. This raises the intriguing question of whether the giant-petrels' ability to obtain food for their chicks rapidly (at high energetic cost) has caused selection for their occupation of high-latitude breeding sites, or whether their use of high-latitude breeding sites has caused selection for rapid and energetically-expensive food gathering for chicks, as suggested for Wilson's Storm-Petrels (Obst, unpubl. data).

Giant-petrels and albatrosses superficially exhibit marked morphological and behavioral similarities that have been interpreted to represent evolutionary convergences in response to selective pressures on these largest of volant seabirds to make use of ambient wind energy for propulsion. In fact, the wing morphology and reproductive strategy of giant-petrels may be determined more directly by trends within their own family. The more subtle differences in details of flight morphology and reproductive strategy that set the two groups apart may ultimately

be of greater importance in shaping distributions and feeding specializations, as mediated through their energetic consequences.

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