

# Behavioural factors affecting foraging effort of breeding wandering albatrosses

SCOTT A. SHAFFER\*, DANIEL P. COSTA\*, and HENRI WEIMERSKIRCH†

\*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064, USA; and

†Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France

## Summary

1. The study examined the behavioural factors that influence variation in foraging costs of wandering albatrosses (*Diomedea exulans* Linnaeus) during two consecutive years. This was performed by measuring simultaneously foraging activities and metabolic rates ( $W\text{ kg}^{-1}$ ) of breeding birds during the incubation periods of 1998 and 1999.

2. A total of 38 birds (19 in each year) were injected with doubly labelled water, equipped with satellite transmitters to measure foraging distance and flight speed, and equipped with activity recorders to measure landings and take-offs from the water surface.

3. In 1999, birds spent on average 30% more time at sea ( $11.07 \pm 3.53$  SD, days), travelled 43% further ( $5473 \pm 2348$  SD, km) and increased the number of landings and take-offs per day by 66% ( $28.1 \pm 11.4$  SD, landings per day) compared to 1998.

4. Energy expenditure rates during foraging were significantly higher in 1999 ( $5.3 \pm 0.8$  SD,  $W\text{ kg}^{-1}$ ,  $n = 8$ ) compared to 1998 ( $4.5 \pm 0.5$  SD,  $W\text{ kg}^{-1}$ ,  $n = 11$ ).

5. Landing and take-off rates explained the greatest proportion of variation in energy expenditure rates of wandering albatrosses, rather than total distance travelled, flight speed or time in flight.

6. Despite 18% higher foraging costs in 1999, the daily rate of food intake was similar between years, suggesting that energy acquisition per unit effort was lower.

7. The energetic cost of flight for wandering albatrosses was estimated to fall between 3.4 and 5.1  $W\text{ kg}^{-1}$ , or 1.4–2.0  $\times$  measured BMR, one of the lowest flight cost yet reported for any seabird.

*Key-words:* cost of flight, doubly labelled water, foraging ecology, interannual variability, satellite tracking.

*Journal of Animal Ecology* (2001) **70**, 864–874

## Introduction

Energy budgets are fundamental to the study of reproductive strategies and life history patterns of organisms (Calow 1979; Walsberg 1983; Stearns 1992). Important components of the energy budget are those activities associated with energy acquisition and expenditure (Sibly & Calow 1986). Moreover, life history theory predicts a trade-off between foraging costs and investment in reproduction (Costa 1991; Stearns 1992). One group of organisms that have taken the trade-off between the energy invested in reproduction and foraging costs to the extreme could be pelagic seabirds of

the order Procellariiformes (albatrosses and petrels). These seabirds exhibit characteristically low reproductive output by laying single egg clutches (Lack 1968). This may be indicative of a limitation on seabird parents to deliver sufficient energy to raise more than one offspring, due either to the scarcity of resources in the environment or the high cost of exploiting distant resources. Albatrosses and petrels generally have low mass-specific field metabolic rates (FMR) (Nagy, Girard & Brown 1999).

Foraging costs often vary in response to changing environmental conditions. Many studies have addressed seasonal and annual variations in foraging effort; however, the underlying behavioural adjustments that are responsible for changes in foraging cost are not well documented. This is mainly attributable to the difficulty of measuring simultaneously behaviour and energetics in free-ranging animals, particularly birds. Most studies that have successfully linked behaviour

Correspondence: Dr Scott A. Shaffer, Department of Ecology and Evolutionary Biology, Long Marine Lab – Center for Ocean Health, University of California Santa Cruz, 100 Shaffer Road, Santa Cruz, California 95060, USA. E-mail: shaffer@biology.ucsc.edu

and energy expenditure involved species that were observed at close range in their natural habitat (Bryant & Westerterp 1980; Reyer & Westerterp 1985; Masman, Daan & Dijkstra 1988). This is more difficult in birds that forage over large spatial scales, particularly seabirds. Despite this, the behaviour of free-ranging seabirds has been recorded by equipping birds with archival data loggers (Nagy, Siegfried & Wilson 1984; Chappell *et al.* 1993a; Weimerskirch, Doncaster & Cuenot-Chaillet 1994). For most birds, which are small, such recorders would significantly alter foraging behaviour. However, larger birds such as albatrosses and penguins are capable of carrying a range of devices without apparent adverse effects, so it is possible to study both the behaviour and energetics of individuals in the wild (Nagy *et al.* 1984; Costa & Prince 1987; Chappell *et al.* 1993b; Bevan *et al.* 1995; Arnould *et al.* 1996).

Previous studies have documented environmental variability by observing changes in foraging behaviour, provisioning rates and body condition of adult albatrosses and petrels (Weimerskirch, Mougey & Hindermeier 1997b; Weimerskirch, Fradet & Chérel 1999). Although these studies demonstrated that variation (natural or experimental) caused adults to modify foraging effort, none of the studies measured energy expenditure directly. There have been a few studies that have measured differences in energy expenditure between stages of the reproductive cycle (Ricklefs, Roby & Williams 1986; Obst, Nagy & Ricklefs 1987; Golet, Irons & Costa 2000), but these studies did not quantify specific details about foraging behaviour (e.g. distance travelled, time in flight, foraging location). Conversely, only three studies have measured simultaneously energy expenditure and foraging behaviour (Bevan *et al.* 1995; Arnould *et al.* 1996; Weimerskirch *et al.* 2000). However, none of these studies addressed seasonal and or interannual variability, yet this variation probably has a significant influence on foraging effort. Therefore, the present study focused on the correlates between foraging behaviour and energy cost and its association with interannual variability in foraging conditions for wandering albatrosses.

Wandering albatrosses are an excellent species in which to examine foraging behaviour and energy expenditure because these birds can be equipped with self-contained archival data loggers and satellite transmitters that measure foraging activity and location. They are the largest procellariiform seabird (8–10 kg) and they exhibit one of the lowest mass-specific FMRs measured of any flighted seabird (Adams, Brown & Nagy 1986; Arnould *et al.* 1996). Therefore, the objective of this study was to examine for the first time the behavioural factors that influence variability in foraging metabolic rate of breeding wandering albatrosses during two consecutive years. This was carried out by evaluating the specific behaviours that influenced overall energy expenditure (e.g. frequency of landings and take-offs, time in flight, foraging location, distance

travelled and speed of travel). Given that we obtained detailed information on activity budgets, we also estimated the cost of flight for wandering albatrosses and compared them to the flight costs for other seabird species.

## Materials and methods

The study was conducted during the austral summers of 1998 and 1999 on Possession Island, Crozet Archipelago, south-western Indian Ocean (46°S, 52°E). The climate in this region is typically cool ( $9.6 \pm 4.2$  °C) and rainy with persistent westerly winds. The study was conducted during the late incubation period in 1998 and the early incubation period in 1999. The main reason for studying the birds during the incubation period was the greater predictability of foraging trip lengths compared to trips made during the chick-rearing period (Weimerskirch *et al.* 1993).

In 1998, 19 birds (10 males and nine females) were studied from mid-February to mid-March and in 1999 another 19 birds (12 males and seven females) were studied from early January to mid-February. The sex of each bird was determined by plumage characteristics (Weimerskirch, Lequette & Jouventin 1989) and from banding and breeding records (Weimerskirch & Jouventin 1987). Because most birds breeding on Crozet were banded as chicks, it was possible to establish the age and prior reproductive history of all study animals. The mean age of males in this study was  $22.4 \pm 8.9$  (SD) years and the mean for females was  $18.4 \pm 9.3$  (SD) years. All but four birds (three in 1998 and one in 1999) in this study had prior breeding experience.

## AT-SEA METABOLIC RATES AND ENERGY EXPENDITURE

Doubly labelled water (DLW) was used to determine at-sea metabolic rates and water influx rates of wandering albatrosses (Lifson & McClintock 1966; Nagy & Costa 1980; Nagy 1980; Speakman 1997). All birds were captured off the nest just after relief by their partner. A cloth hood was placed over the head, and 3–4 mL of blood was sampled from a vein on the tarsus. Albatrosses were given an intraperitoneal (i.p.) injection of 15–20 mL of sterile water containing 10 atom percentage oxygen-18,  $2.15 \text{ MBq mL}^{-1}$  of tritiated water and 0.9% NaCl. The mass of the injected volume was determined by weighing the syringe ( $\pm 0.01$  g) before and after injection. Each bird was weighed to the nearest 50 g using a Salter spring balance (Salter Weightronix Ltd, West Bromwich, UK). All birds were released close to their nests during isotope equilibration. Albatrosses attempting to depart were captured and held for the remainder of the equilibration period, which was determined to be 100 min. The time for equilibration of isotopes was determined in a separate study on incubation energetics of wandering albatross (Shaffer 2000; Shaffer, Costa & Weimerskirch in review). In this study,

five adults were injected with tritiated water, and then blood was sampled every 30–45 min for a total of 160 min. In all cases, isotopes were completely equilibrated with body water within 100 min of injection. Following equilibration, each bird was recaptured and 4–6 mL of blood was collected from a tarsal vein. A satellite transmitter and wet–dry logger were attached (described below), and the bird was released close to its nest. Upon returning from sea, injected birds were recaptured after relieving their mate. A final 4–6 mL blood sample was collected from a tarsal vein and final body mass was measured.

All blood samples were collected with a syringe, transferred to a vacutainer (B-D brand with no additives; Beckton-Dickinson, Franklin Lakes, NJ, USA) and stored at 5–8 °C for several hours. After centrifugation, serum was transferred to 2 mL plastic screw-cap vials (with silicon o-rings; Sarstedt, Inc., Newton, NC, USA) and frozen at –5 °C until analyses were performed in May (1998) and April 1999 for each season's samples, respectively. The specific activity of tritiated body water was determined in triplicate by scintillation spectrometry (Beckman LS 6500, Beckman Coulter Inc., Fullerton, CA, USA) of ~90 µL of water in 10 mL of Ecolite + scintillation cocktail (ICN Pharmaceuticals, Costa Mesa, CA, USA). Water was obtained by distilling 100 µL aliquots of serum following methods described in Ortiz, Costa & Le Boeuf (1978). Specific activity of oxygen-18 water was determined by mass ratio spectrometry of water distilled from blood serum (Metabolic Solutions, Nashua, NH, USA).

Initial total body water was calculated using the initial dilution space of oxygen-18. Final body water content was estimated as the initial fractional water content × the final body mass (Nagy 1983; Speakman 1997). Rates of CO<sub>2</sub> production were determined using equation 2 in Nagy (1980) and water influx was calculated using equations 4 and 6 in Nagy & Costa (1980). These equations assume that an animal's body mass, and therefore body water volume, change linearly through time (Nagy 1983).

Carbon dioxide production was converted to units of energy expenditure in kilojoules (kJ) using a conversion factor of 1 L CO<sub>2</sub> = 25.2 kJ (Adams *et al.* 1986). This conversion factor was based on the chemical composition of a squid and fish diet consumed by albatrosses (Clarke & Prince 1979; Croxall & Prince 1980; Croxall & Prince 1982). Mass-specific FMR was calculated by dividing a bird's FMR in watts (W) by its body mass (kg) raised to the power of 1.0, because FMR scaled isometrically with body mass for wandering albatrosses ( $\log_{10} \text{watts} = 0.694 + 0.980 \log_{10} \text{kg}$ ;  $F_{1,52} = 38.2$ ,  $P < 0.001$ ,  $r^2 = 0.424$ ). This equation was generated using data from the present study and that of Adams *et al.* (1986) and Arnould *et al.* (1996). Unless stated otherwise, comparisons between FMR and BMR (i.e. basal metabolic rate) were made using measured BMR (2.5 W kg<sup>-1</sup>) determined by Brown & Adams (1984). Water influx rates were used as a proxy for food

consumption, assuming that preformed water in food and metabolic water production comprise the only sources of water intake.

Time at sea was determined by direct observation of departure and return times to the colony, and/or by the analysis of activity recorder data and satellite positions. Because DLW measurement intervals included brief periods ashore (birds were either on or near their nest), at-sea energy expenditure (W kg<sup>-1</sup>) was corrected following the methods of Costa & Prince (1987). At-sea metabolic rate (MR) = [measured MR – (incubation MR × proportion of time ashore)]/proportion of time at sea]. Metabolic rates of incubating wandering albatrosses (six males and four females) were determined using DLW in a study conducted in January–February 1999. The combined mean energy expenditure for incubating birds was 2.0 ± 0.2 W kg<sup>-1</sup> (Shaffer *et al.* in review).

Field metabolic rates were determined for 11 out of 19 birds (seven males and four females) injected with DLW during 1998 and eight of 19 birds (seven males and one female) injected with DLW during 1999. The remaining birds were at sea for 11 days or longer, particularly in 1999, so their final oxygen-18 values were too close to background levels to permit accurate measurements of metabolism. However, water flux was measured in 31 out of the original 38 birds injected with DLW, because tritiated water levels were sufficiently above background to permit accurate water flux determinations.

#### AT-SEA FORAGING BEHAVIOUR AND ACTIVITY PATTERNS

The movement patterns of injected birds were studied using satellite platform terminal transmitters (PTT 100, Microwave Telemetry, Columbia, MD, USA). Each bird was equipped with a 20- or 30-g PTT attached to feathers on the back with white adhesive tape (Weimerskirch *et al.* 1994). Six to 12 geographical locations from each bird were obtained and processed daily by Argos (CLS Argos, Toulouse, France). Analysis of satellite fixes was performed using ELSA software (CLS Argos, Toulouse, France) after data were filtered according to procedures described in Weimerskirch *et al.* (1993). For each trip to sea, we determined (1) foraging location, (2) total straight line distance flown as well as distance flown per day, (3) maximum distance or range from the colony and (4) average flight speeds (i.e. ground speed) between fixed locations. Interannual differences in foraging locations were analysed by establishing foraging sectors N or S and E or W of Ile de la Possession. For each trip, the difference in latitude and longitude of each satellite fix was subtracted from the latitude and longitude of the island. All differences for a single trip were reduced to a single mean difference in latitude and longitude. If the mean difference in latitude was positive (i.e. latitude increased), then the bird was predominately foraging south of the

**Table 1.** Interannual comparisons of foraging behaviour and energy expenditure of breeding adult wandering albatrosses. All values are means  $\pm$  SD and sample sizes are given in parentheses. Intra-annual sex differences in body mass were highly significant  $P < 0.001$ 

Parameter		1998	1999	Test	<i>P</i>
Initial mass (kg)	M	10.73 $\pm$ 0.71 (10)	9.57 $\pm$ 0.45 (12)	$t = 4.66$	$< 0.001$
	F	8.92 $\pm$ 0.50 (9)	7.88 $\pm$ 0.41 (7)	$t = 4.47$	0.001
Time at sea (d)	C	8.51 $\pm$ 3.67 (19)	11.07 $\pm$ 3.53 (19)	$t = -2.19$	0.035
Total distance (km)	C	3834 $\pm$ 2134 (17)	5473 $\pm$ 2348 (14)	$t = -2.04$	0.051
Daily distance (km d <sup>-1</sup> )	C	469 $\pm$ 129 (17)	519 $\pm$ 135 (14)	$t = -1.05$	0.304
Maximum range (km)	C	843 $\pm$ 333 (17)	1255 $\pm$ 544 (14)	$t = -2.59$	0.015
Flight speed (km h <sup>-1</sup> )	C	24.1 $\pm$ 4.8 (17)	27.5 $\pm$ 5.1 (14)	$t = -1.88$	0.071
Maximum flight speed (km h <sup>-1</sup> )	C	78.5 $\pm$ 7.2 (17)	82.7 $\pm$ 7.7 (14)	$t = -1.56$	0.131
Time in flight (% of trip)	C	46.3 $\pm$ 7.7 (16)	47.4 $\pm$ 6.4 (17)	$t = -0.47$	0.639
Landings per day	C	16.9 $\pm$ 9.8 (16)	28.1 $\pm$ 11.4 (15)	$t = -2.96$	0.006
Total mass change (% body mass)	C	8.0 $\pm$ 7.0 (18)	13.3 $\pm$ 7.8 (19)	$t = -2.02$	0.052
Daily mass change (kg d <sup>-1</sup> )	C	0.11 $\pm$ 0.09 (18)	0.11 $\pm$ 0.06 (19)	$t = 0.07$	0.942
Total body water (%)	C	47.7 $\pm$ 3.4 (19)	51.2 $\pm$ 2.6 (19)	$t = -3.54$	0.001
CO <sub>2</sub> production (mL g <sup>-1</sup> h <sup>-1</sup> )	C	0.61 $\pm$ 0.06 (11)	0.72 $\pm$ 0.10 (8)	$t = -3.05$	0.007
Absolute FMR (W)	C	47.7 $\pm$ 6.3 (11)	52.9 $\pm$ 6.7 (8)	$t = -1.73$	0.102
Mass-specific FMR (W kg <sup>-1</sup> )	C	4.5 $\pm$ 0.5 (11)	5.3 $\pm$ 0.8 (8)	$t = -2.55$	0.021
Water influx rate (mL d <sup>-1</sup> )	C	1232 $\pm$ 281 (14)	1341 $\pm$ 377 (17)	$t = -0.90$	0.376

F, female; M, male; C, combined sexes; FMR, field metabolic rate; W, watts; kg, kilograms; mL, millilitres; km, kilometres; d, days; h, hours.

island. Similarly, if mean longitude was positive (i.e. longitude increased) then the bird foraged east of the island. Two  $\times$  two contingency tables were used to test for associations between year and foraging sector.

In addition to studying movement patterns, we also quantified the foraging activity of injected birds using a 25-g wet-dry activity data logger (Francis Scientific Instruments, Cambridge, UK). The loggers were fixed to the bird's tarsus by taping the logger to a plastic identification band. Loggers were programmed to sample for 1 s every 7.5 or 15 s to detect whether the unit was wet or dry, and these sampling periods were linked to the time of day. Hence, a change in the wet or dry condition represented a landing or take-off from the water. In 1998 only, five injected birds went to sea with a 30-g SECUP logger (DK-log 120, Pillbox Logger, Driesen + Kern GmbH, Germany) instead of a wet-dry logger. The SECUPs operated by recording changes in temperature associated with air or water at 32-s intervals. Details of the loggers and analysis procedures are described in Wilson, Weimerskirch & Lys (1995). Thus, for each trip to sea made by the albatrosses, we were able to quantify (1) percentage of time in flight and on water, (2) frequency of landings (per trip or per day) and (3) diurnal foraging activity.

Statistical analyses were performed using SYSTAT 9.0 (Wilkinson 1996) with a significance level of  $P \leq 0.05$  for  $t$ -tests (two tailed), contingency tables, Pearson product-moment correlations, regression analyses and ANOVAS. Two-way ANOVAS were used initially to examine interactions between sex and year. However, in all cases except body mass, there were no interactions, so the results of  $t$ -tests were presented instead. Statistical analyses of proportional data (e.g. % mass change, % total body water and % time in flight) were performed after the data were arcsine-transformed. Tests for asso-

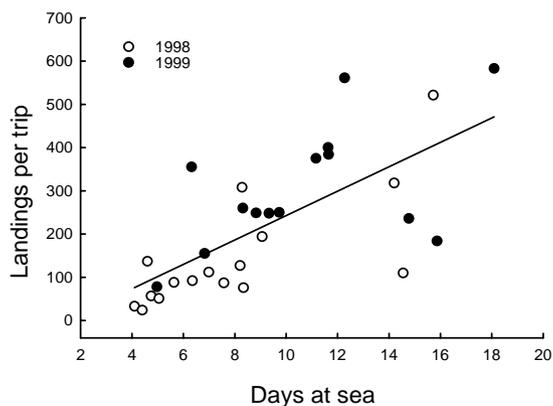
ciations between foraging sectors and years were analysed with contingency tables by performing a  $G$ -test (log-likelihood ratio test) for independence with the Williams correction (Sokal & Rohlf 1981). Unless stated otherwise, all data are presented as means  $\pm$  1 standard deviation (SD).

## Results

Body mass was approximately 20% greater in males compared to females (Table 1). For both years combined, absolute FMR was significantly higher in males compared to females (males: 51.7  $\pm$  6.2 W vs. females: 44.6  $\pm$  6.1 W;  $t = -2.23$ , d.f. = 17,  $P = 0.040$ ), but this was attributed to body size differences because mass-specific FMR (W kg<sup>-1</sup>) was not significantly different between the sexes. The only foraging behaviour that was significantly different between males and females was the percentage of time in flight; for both years combined, males spent proportionately less time in flight and more time on the water than females (males: 49.8  $\pm$  11.4% vs. females: 58.5  $\pm$  11.0%,  $t = 2.14$ , d.f. = 31,  $P = 0.040$ ). No intra-annual sex difference in percentage time in flight was observed. All other data for males and females were combined within years to analyse for interannual differences (Table 1).

## DIFFERENCES IN FORAGING ACTIVITY BETWEEN YEARS

There were distinct differences in foraging behaviour between years. Foraging trips averaged 30.1% (2.5 days) longer in duration in 1999 compared to 1998 (Table 1). The total number of landings made while foraging was also correlated with time at sea when data from both years were combined (Fig. 1;  $F_{1,29} = 26.2$ ,



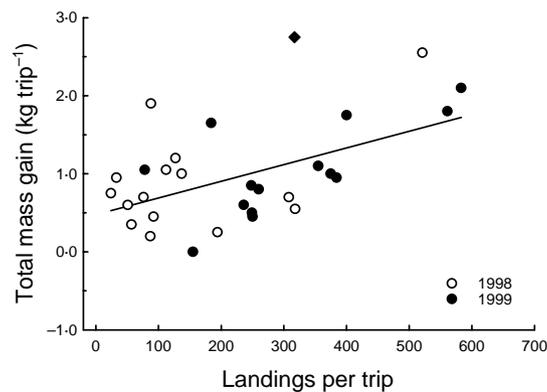
**Fig. 1.** The total number of landings per foraging trip plotted as a function of time at sea for adult wandering albatrosses foraging during the incubation periods of 1998 and 1999 (combined data for both years;  $F_{1,29} = 26.2$ ,  $P < 0.001$ ,  $r^2 = 0.475$ ).

$P < 0.001$ ,  $r^2 = 0.475$ ). Albatrosses travelled on average 43% further per foraging trip in 1999 compared to 1998, although the difference was marginally significant ( $P = 0.051$ ; Table 1). Nevertheless, the daily rate of travel was similar between years (Table 1). The average maximum foraging range from the breeding colony in 1999 was about 50% further than in 1998 (Table 1). Mean flight speeds were not significantly different between years, although there was a trend towards greater flight speed in 1999 (Table 1). In both years, average maximum flight speed was approximately  $80 \text{ km h}^{-1}$  (Table 1). The most striking difference in foraging activity between years was in landings per day, which averaged 66% higher in 1999 compared to 1998 (Table 1).

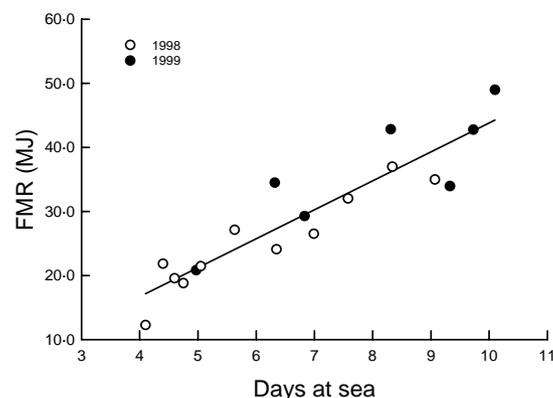
In addition to differences in foraging activity, wandering albatrosses appeared to use different foraging sectors in the two years. There was a greater frequency of birds that foraged south of Crozet in 1999 (9 S vs. 5 N) compared to the number of birds that foraged south of the island in 1998 (5 S vs. 13 N;  $G = 4.138$ , d.f. = 1,  $P = 0.042$ ). No significant associations in longitude were observed in either year ( $G = 1.579$ , d.f. = 1,  $P = 0.209$ ). Despite the fact that birds foraged in different oceanic sectors, we could not rule out the possibility that between-year variation resulted from differences in the timing of the study (i.e. early vs. late incubation) because the foraging behaviour of wandering albatrosses changes throughout the year (Tickell 1968; Weimerskirch *et al.* 1993).

#### DIFFERENCES IN FORAGING EFFORT RELATED TO ENERGY EXPENDITURE

Foraging activity was correlated with the acquisition of food and energy expenditure, both in terms of absolute differences between years and the frequency of landings. There was a tendency for birds to gain more mass in 1999 compared to 1998 (Table 1). Total mass gained was weakly positively correlated with the number of



**Fig. 2.** Total mass gained as a function of landings per trip in adult wandering albatrosses foraging during the incubation periods of 1998 and 1999 ( $F_{1,28} = 11.3$ ,  $P = 0.002$ ,  $r^2 = 0.287$ ). The solid diamond was an outlier and not included in the analysis. This bird spent 63% of its time on the water while at sea, which was well above the mean (~50%) exhibited by other males in this study (Table 1).



**Fig. 3.** The change in total energy expenditure (megajoules; MJ) as a function of time at sea in days of adult wandering albatrosses breeding in 1998 and 1999 ( $F_{1,17} = 103$ ,  $P < 0.001$ ,  $r^2 = 0.859$ ).

landings per trip (Fig. 2;  $F_{1,28} = 11.3$ ,  $P = 0.002$ ,  $r^2 = 0.287$ ) as well as the duration at sea ( $F_{1,35} = 9.1$ ,  $P = 0.005$ ,  $r^2 = 0.206$ ).

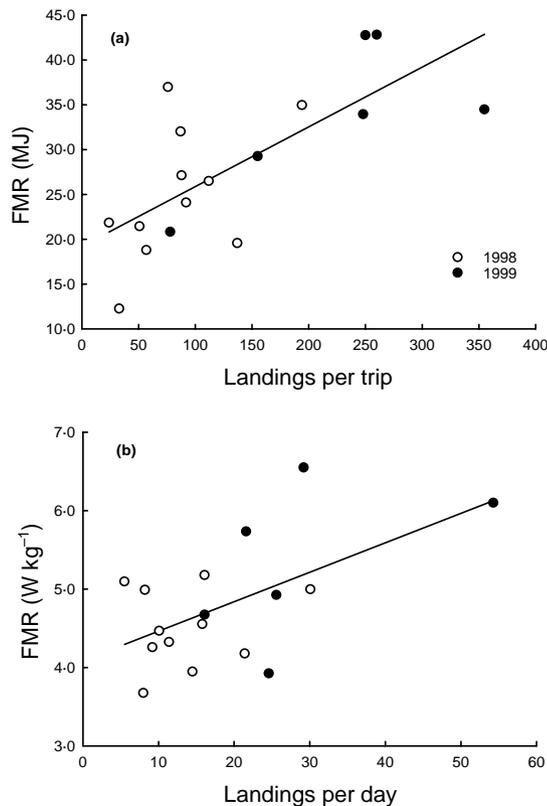
Mean absolute FMR (W) was not significantly different between years; however, mean  $\text{CO}_2$  production ( $\text{mL g}^{-1} \text{ h}^{-1}$ ) and mass-specific FMR ( $\text{W kg}^{-1}$ ) were significantly higher in 1999 (Table 1). Because birds were at sea for significantly longer periods in 1999, total foraging costs per trip (megajoules; MJ) were higher in 1999 ( $37.3 \pm 9.4 \text{ MJ}$ ) compared to 1998 ( $25.1 \pm 7.4 \text{ MJ}$ ;  $t = -3.18$ , d.f. = 17,  $P = 0.006$ ). Total energy expenditure (MJ) was also positively correlated with time at sea (Fig. 3 and Table 2;  $F_{1,17} = 103$ ,  $P < 0.001$ ,  $r^2 = 0.859$ ); however, the rate of energy expenditure ( $\text{W}$  or  $\text{W kg}^{-1}$ ) was not correlated with time at sea.

The difference in mass-specific energy expenditure rate between years appeared to be related to the number of landings that albatrosses made per day while foraging. Total energy expenditure per trip (MJ) was positively correlated with the number of landings per trip (Fig. 4a, Table 2;  $F_{1,15} = 16.5$ ,  $P = 0.001$ ,

**Table 2.** Comparison of Pearson product-moment correlations with field metabolic rates ( $W\text{ kg}^{-1}$  or MJ) and foraging activity. Correlations were tested with data from both years combined

Parameter	FMR ( $W\text{ kg}^{-1}$ )		FMR (MJ)	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Time at sea (d)	0.114	0.642	0.927	0.000
Time in flight (%)	0.346	0.147	-0.030	0.904
Total distance (km)	0.160	0.539	0.700	0.002
Daily distance ( $\text{km d}^{-1}$ )	-0.012	0.964	0.190	0.464
Mean flight speed ( $\text{km h}^{-1}$ )	0.093	0.724	0.336	0.187
Maximum flight speed ( $\text{km h}^{-1}$ )	-0.077	0.768	0.604	0.010
Landings	0.570*	0.017*	0.724†	0.001†

W, watts; MJ, megajoules; kg, kilograms; d, days; h, hours; km, kilometres. \*Landings per day. †Landings per trip.



**Fig. 4.** Energy expenditure in relation to foraging behaviour of adult Wandering Albatrosses foraging during the incubation periods of 1998 and 1999. (a) Total energy expenditure (megajoules; MJ) as a function of landings per trip ( $F_{1,15} = 16.5$ ,  $P = 0.001$ ,  $r^2 = 0.524$ ). (b) Daily energy expenditure (Watts;  $W\text{ kg}^{-1}$ ) as a function of landings per day ( $F_{1,15} = 7.2$ ,  $P = 0.017$ ,  $r^2 = 0.325$ ). Energy expenditure was measured with doubly labelled water and landings were measured with wet-dry data loggers.

$r^2 = 0.524$ ). Similarly, mass-specific FMR ( $W\text{ kg}^{-1}$ ) was positively correlated with the number of landings per day (Fig. 4b,  $F_{1,15} = 7.2$ ,  $P = 0.017$ ,  $r^2 = 0.325$ ). Remarkably, no other foraging behaviours were significantly correlated with mass-specific FMR (Table 2). To investigate whether multiple factors (i.e. behaviours) influenced mass-specific FMR, a stepwise multiple linear regression was performed using four covariates: (1) landings per day, (2) daily distance

flown, (3) average flight speed and (4) percentage of time in flight. Together, these four covariates explained 60.5% of the total variation in mass-specific FMR as described by the equation:

$$\begin{aligned} W\text{ kg}^{-1} = & 2.39 - 0.006 * \text{distance} + 0.120 * \text{speed} \\ & + 0.032 * \% \text{ time} + 0.04 * \text{landings} \\ (F_{4,10} = & 6.37, P = 0.008, r^2 = 0.605). \end{aligned}$$

Of the four covariates, only landings per day was significant and it explained the greatest variation ( $F_{1,15} = 10.1$ ,  $P = 0.010$ ,  $r^2 = 0.336$ ). The remaining covariates in decreasing order of importance were percentage of time in flight ( $r^2 = 0.127$ ), daily distance flown ( $r^2 = 0.092$ ) and average flight speed ( $r^2 = 0.032$ ).

Lastly, there was a significant difference in the body condition of adults between years. Initial body masses of both male and female wandering albatrosses were significantly greater (~13%) in 1998 compared to 1999 (Table 1). Furthermore, percentage of total body water was significantly lower (~7%) for adults in 1998 than in 1999 (Table 1), suggesting that adults were in poorer body condition in 1999.

## Discussion

We were able to document for the first time the specific foraging behaviours that influence the energy expenditure of a free-ranging seabird. This was made possible because foraging effort was studied during two contrasting periods when variations in energetics and behaviour increased the probability of detecting a pattern. In the present study, daily mass gain measured at the end of a foraging trip was identical between years, indicating that energy yield per unit time was similar. Water influx rates, which are an approximate measure of prey intake, were also similar between years; however, energy expenditure rates were higher in 1999 (Table 1). This discrepancy could be due either to the inability to detect a significant difference in water influx rates (1999 > 1998 but not significant), or that the prey quality differed between years. In the absence of data on prey quality, we have to assume that both years were similar. However, the fact that foraging costs were

higher in 1999 yet daily mass gain was the same in both years indicates that foraging efficiency was lower in 1999. In other words, the increase in landings and take-offs per day was not matched by an increase in the energy yield per landing; thus, the rate of patch utilization was different between years.

The fact the birds appeared to be in poorer body condition in 1999 may also reflect differences in foraging efficiency between study periods. If adults were not able to recover sufficient body reserves while foraging then they would certainly be in poorer condition when finishing an incubation bout, which is consistent with our measurements of higher total body water in 1999. The difference in body condition may have also influenced foraging behaviour of adults in 1999. Hence, because adults had lower body mass and higher percentage of TBW, it is conceivable that albatrosses increased foraging effort (i.e. duration and cost) to replenish body reserves.

The results from our first year were consistent with previous estimates of daily energy expenditure in wandering albatrosses (Adams *et al.* 1986; Arnould *et al.* 1996). However, given that mass-specific FMR ( $\text{W kg}^{-1}$ ) during the incubation period differed between years, we now know that mass-specific FMR varies from 1.8 to  $2.1 \times$  measured BMR. Despite the significant between-year difference in foraging effort, reproductive success (% of chicks fledged from eggs laid) was similar in both years (1998 = 76.6% vs. 1999 = 71.6%,  $\chi^2 = 2.495$ , d.f. = 1,  $P = 0.114$ ), and comparable to the 26-year average of  $68.5 \pm 11.2\%$  at Crozet (Weimerskirch, Brothers & Jouventin 1997a).

#### BEHAVIOURAL FACTORS INFLUENCING FORAGING EFFORT

Of those foraging behaviours that we measured in wandering albatrosses, the one most closely associated with foraging effort was the rate of landings and take-offs (Table 2). Further support for our conclusion was provided in another study that measured heart rates in free-ranging wandering albatrosses (Weimerskirch *et al.* 2000). This study showed that heart rates increased by 3–4 times over resting levels when birds ran, landed or took off from the water surface compared to birds engaged in prolonged periods of flight, where heart rates averaged  $\sim 1.4 \times$  resting levels. The heart rate study and the results of our study indicate that landings and take-offs (i.e. flapping flight) are energetically expensive for albatrosses. Flapping flight requires a high power output for wandering albatrosses because of their long, narrow wings, which produce low thrust at slow speeds (Pennycuick 1989), especially when taking off or landing. Predicted power output of flapping flight in wandering albatrosses is approximately  $30 \times$  BMR (Alerstam, Gudmundsson & Larsson 1993; BMR determined with allometric equation of Lasiewski & Dawson (1967)). Thus, although the cost of flight is extremely low for wandering albatrosses (see

below), there is a clear trade-off with flapping flight, which is very costly and used mainly during landings or take-offs.

Albatrosses exploit wind energy to soar at a low cost (Wilson 1975; Pennycuick 1982). Predictions based on aerodynamic principles suggest that birds of this size and mass require strong winds to achieve optimal gliding performance (Pennycuick 1989). Our analysis showed that flight speed was not correlated with energy expenditure; therefore, wind conditions must have been sufficient during both years to enable soaring at a low cost. When winds are too low to enable soaring, however, wandering albatrosses typically remain on the water until more favourable wind conditions prevail (Jouventin & Weimerskirch 1990). There was no interannual difference in the percentage of time that either males or females spent on the water, results that are consistent with those of previous studies (Weimerskirch, Wilson & Lys 1997c).

Although time at sea and distance flown differed substantially between years, they did not correlate with mass-specific FMR (Table 2;  $\text{W kg}^{-1}$ ). However, time at sea was significantly correlated with total energy expenditure (MJ), which was related to the greater number of landings made on longer foraging trips (Figs 1 and 4). Because wandering albatrosses forage on patchy ephemeral prey, the total number of encounters with prey should increase with time at sea and area searched (Weimerskirch *et al.* 1997c). Even though mass-specific FMR did not increase with time at sea, total energy expenditure should increase with foraging bout length simply because birds are likely to encounter more prey and thus perform more landings and take-offs when at sea for longer periods.

#### VARIABILITY DUE TO METHODOLOGICAL ERROR

Speakman (1997) reviewed the number of DLW validation studies on animals ( $N = 46$ , of which 16 were conducted on birds) and humans ( $N = 29$ ) and determined that the cumulative mean algebraic error in  $\text{CO}_2$  production was  $+1.36 \pm 6.4\%$  SD compared to other methods (e.g. respirometry). However, the individual variation in relation to other methods could be high ( $-38\%$  to  $+54\%$ ). Unfortunately, there are no studies that have compared metabolic rate using DLW and respirometry in wandering albatrosses, so we can only assume that our measurements are within the range of other studies. The results of the present study exhibited coefficient of variations in mean  $\text{CO}_2$  production of 10–14% (1998 and 1999, respectively). We are aware of only one study that validated DLW against respirometry measurements for an albatross species (black-browed albatrosses, *Thalassarche melanophrys* Temminck; Bevan *et al.* 1995). For measurements of six individuals, the mean algebraic error was 4–10% depending on the equation used, and individual variation ranged from  $-21\%$  to  $+41\%$ .

Since the development of the original equations by Lifson & McClintock (1966), there are at least eight equations for calculating CO<sub>2</sub> production from DLW (Speakman 1997). One set of equations (Nagy 1980) uses a single pool model and corrects for errors associated with large variations in the animal's body water pool. This equation adjusts for changes in water space of at least 20% without a resultant error in CO<sub>2</sub> production (Nagy 1980). The other equations use either a single or a two-pool model and correct for errors caused by physical fractionation of the oxygen and hydrogen isotopes. Corrections for physical fractionation assume that the rate of isotope fractionation is constant under physiological conditions. In addition, the environment of a free-ranging animal is rarely constant, especially for wandering albatrosses that forage from the subtropics to Antarctic waters (Prince *et al.* 1992; Weimerskirch *et al.* 1993). Regardless, there are no equations that correct for errors due to both fractionation and changing water space (K. A. Nagy personal communication). Given that the average change in body mass of our study animals was 8–13% (Table 1), we felt that it would be more important to correct for errors associated with changing mass (i.e. water space) than physical fractionation (Nagy 1980). Further, validation studies show good agreement when changes in body mass are corrected for, while fractionation of tritium and oxygen-18 are not (Buttemer *et al.* 1986; Gales 1989). If we compare CO<sub>2</sub> production using the two-pool model (eqn 7.44 Speakman 1997) and the Nagy (1980) equation on our data, we find that relationships between energy expenditure and foraging behaviour are more robust when CO<sub>2</sub> production is calculated with the Nagy equation. When using FMR calculated with the two-pool model, the relationship between daily energy expenditure (W kg<sup>-1</sup>) and number of landings per day is more variable and barely significant ( $F_{1,15} = 4.44$ ,  $P = 0.052$ ,  $r^2 = 0.229$ ) and the relationship between total energy expenditure (MJ) and number of landings per trip is significant, but also more variable ( $F_{1,15} = 10.6$ ,  $P = 0.005$ ,  $r^2 = 0.413$ ).

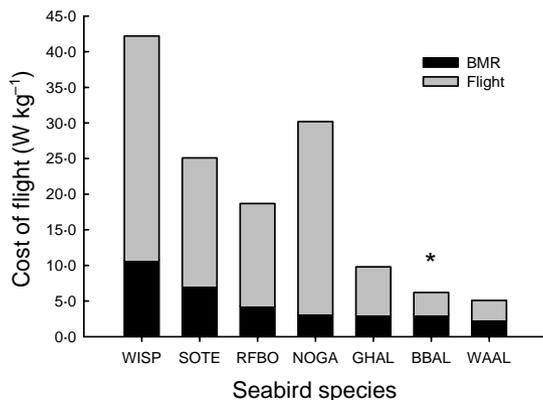
It is common practice when using DLW to assume that the fractional body water content (%TBW) remains constant over the measurement interval (Adams *et al.* 1986; Costa & Prince 1987; Arnould *et al.* 1996; Speakman 1997). None the less, we attempted to verify this by re-determining water space at the end of the measurement interval. Our attempts resulted in a bird abandoning its egg. Given that wandering albatrosses are biennial breeders with a population status that is considered vulnerable (Alexander, Robertson & Gales 1997), we aborted further attempts at directly measuring final water space. However, Shaffer *et al.* (in review) measured TBW of incubating adults (six males and four females) within 12–24 h after a foraging trip. The mean percentage of TBW was 48.9%, which was not statistically different from the birds that were captured before heading to sea.

Although a low TBW gives the impression that wan-

dering albatrosses are really fat, it has been suggested that their long wings and flight feathers contribute to the low TBW, because they are dry tissues that are part of the overall mass but not water space (Adams *et al.* 1986). In comparison to other albatrosses and petrels, our measurements of TBW are similar to those published in other studies (TBW 44.5–57.9%; see review Speakman 1997).

#### COST OF FLIGHT

That wandering albatrosses can fly thousands of kilometres in only a few weeks (i.e. 12–13 h per day) demonstrates that dynamic soaring is extremely fast and economical. Pennycuik (1982) estimated that a wandering albatross could travel nearly 1000 km in 29 flight hours and consume only 1% of its body mass in fat. This estimation was based on a power consumption of 2 × metabolic power (i.e. metabolic power being the mechanical equivalent of BMR derived from the equation of Lasiewski & Dawson (1967) as cited in Pennycuik (1982)), which is similar to our measurements of daily energy expenditure (DEE). However, DEE integrates all aspects of a foraging trip (e.g. resting on water, flight and landings). Therefore, we combined data for specific activity and FMR into a multiple linear regression to estimate a revised cost of flight for wandering albatrosses. Cost of flight was estimated by the equation  $W \text{ kg}^{-1} = 3.44 + 0.017 * \% \text{ time in flight} + 0.031 * \text{landings per day}$  ( $F_{2,15} = 3.86$ ,  $P = 0.045$ ,  $r^2 = 0.340$ ). With this equation, we can solve for the cost of flight by setting the time spent flying to 100% and the number of take-offs and landings to zero. The cost of flight would be 5.1 W kg<sup>-1</sup> (i.e.  $W \text{ kg}^{-1} = 3.44 + 0.017 * 100$ ), which is equivalent to 2.0 × measured BMR. An alternative and independent estimate of flight cost can be derived by combining the data of Bevan *et al.* (1995) and Weimerskirch *et al.* (2000). Weimerskirch *et al.* (2000) reported that heart rates of wandering albatrosses in flight were 1.4 times that of an incubating bird. Assuming that the relationship between heart rate and oxygen consumption for wandering albatrosses is similar to black-browed albatrosses, we can use equation 2 of Bevan *et al.* (1995) to estimate that an increase in heart rate of 1.4 times is equivalent to a 1.7 increase in metabolic rate. Therefore, cost of flight would be 1.7 times the cost of an incubating albatross (2.0 W kg<sup>-1</sup>, Shaffer *et al.* in review) or 3.4 W kg<sup>-1</sup>. This value is 1.4 × measured BMR determined by Brown & Adams (1984). A range of 1.4–2.0 × measured BMR is substantially lower than previous estimates of 2.35 × measured BMR (Adams *et al.* 1986) and comparable to or lower than the 2.0 × estimated BMR (using the equation of Ellis 1984) determined by Bevan *et al.* (1995) in black-browed albatrosses. Considering the differences in methodologies employed to measure flight costs, it is reassuring that our estimates are comparable to those of Bevan *et al.* (1995), which used heart rate to predict FMR, and



**Fig. 5.** The cost of flight ( $\text{W kg}^{-1}$ ) of seven seabird species. The black portion represents the basal metabolic rate (BMR) and the cost of flight is the combined total (black + grey). All estimates of flight costs were measured with doubly labelled water and time energy budgets (see references for details), except for the black-browed albatross. Energy expenditure of black-browed albatrosses was determined by measuring heart rates (Bevan *et al.* 1995). For consistency of the comparisons, BMR was estimated using an allometric equation for BMR from Ellis (1984). Species abbreviations and references are as follows: WISP, Wilson storm petrel (Obst *et al.* 1987); SOTE, sooty tern, *Sterna fuscata* Linnaeus (Flint & Nagy 1984); RFBO, red-footed booby (Ballance 1995); NOGA, northern gannet (Birt-Friesen *et al.* 1989); GHAL, grey-headed albatross (Costa & Prince 1987); BBAL, black-browed albatross (Bevan *et al.* 1995); WAAL, wandering albatross (present study).

identical to theoretical predictions of Pennycuik (1982).

When compared to other seabirds, wandering albatrosses have one of the lowest costs of flight yet measured, both in terms of mass-specific FMR and as a multiple of BMR (Fig. 5). One major difference is the proportion of time spent in powered flight, which is small for all albatrosses compared to other species. For example, northern gannets (*Sula bassanus* Linnaeus) use a higher proportion of flapping flight compared to red-footed boobies (*Sula sula* Linnaeus), which exhibit more gliding flight (Birt-Friesen *et al.* 1989; Ballance 1995). Consequently, flight costs are higher in northern gannets (Birt-Friesen *et al.* 1989). Wind and weather also play a significant role in determining flight costs. A lack of wind was shown to increase foraging costs in northern fulmars (*Fulmarus glacialis* Linnaeus; Furness & Bryant 1996), while heavy winds apparently increased FMR in black-legged kittiwakes, *Rissa tridactyla* Linnaeus (Gabrielsen, Mehlum & Nagy 1987). For species that are highly adapted for gliding flight, such as black-browed, grey-headed and wandering albatrosses, the costs of flight are comparatively low in relation to the other seabirds but similar to each other.

## Conclusions

Interannual variability in foraging costs were demonstrated in wandering albatrosses. For the first time, a

specific foraging behaviour was shown to be related to the difference in foraging cost. This variability was related to the frequency of landings or take-offs, and not to how fast they flew or where they foraged. We suspect that variation in the rates of landings and take-offs reflect differences in patch utilization and visitation, and is consistent with the patchy and ephemeral nature of the prey resources for this species. Furthermore, we suggest that the rate of landings and take-offs is a good predictor of foraging effort. The variability in foraging effort demonstrates that wandering albatrosses can respond to annual or seasonal variations in food availability and energy requirements. Estimates of flight costs for wandering albatrosses are among the lowest for seabirds, which clearly illustrates the economy of their soaring flight.

## Acknowledgements

We thank A.E. Hoecker, J. Martin, T. Guionnet and Y. Tremblay for assistance in the field. G. W. Gabrielsen, T.M. Williams, D.A. Croll and K.A. Nagy provided comments on the manuscript. Logistical and financial support came from the National Geographic Society (grant no. 6346–98), National Science Foundation (INT-9873760), and a National Science Foundation Dissertation Improvement Grant (IBN-9972651) to S.A. Shaffer. Logistical and financial support were also provided by the Institut Français pour la Recherche et la Technologie Polaire (IFRTP Program no. 109), and CNRS–NSF funding (99 N92/0214). The appropriate Institutional Animal Care and Use Committees approved all protocols.

## References

- Adams, N.J., Brown, C.R. & Nagy, K.A. (1986) Energy expenditure of free-ranging wandering albatrosses *Diomedea exulans*. *Physiological Zoology*, **59**, 583–591.
- Alerstam, T., Gudmundsson, G.A. & Larsson, B. (1993) Flight tracks and speed of Antarctic and Atlantic seabirds: radar and optical measurements. *Philosophical Transactions of the Royal Society of London B*, **340**, 55–67.
- Alexander, K., Roberston, G. & Gales, R. (1997) *The incidental mortality of albatrosses in longline fisheries*. Technical Report from the First International Conference On The Biology and Conservation of Albatrosses, Hobart, Australia, 1995.
- Arnould, J.P.Y., Briggs, D.R., Croxall, J.P., Prince, P.A. & Wood, A.G. (1996) The foraging behaviour and energetics of wandering albatrosses brooding chicks. *Antarctic Science*, **8**, 229–236.
- Ballance, L.T. (1995) Flight energetics of free-ranging Red-Footed Boobies (*Sula Sula*). *Physiological Zoology*, **68**, 887–914.
- Bevan, R.M., Butler, P.J., Woakes, A.J. & Prince, P.A. (1995) The energy expenditure of free-ranging black-browed albatrosses. *Philosophical Transactions of the Royal Society of London B*, **350**, 119–131.
- Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K. & Macko, S.A. (1989) Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology*, **70**, 357–367.
- Brown, C.R. & Adams, N.J. (1984) Basal metabolic rate and

- energy expenditure during incubation in the wandering albatross (*Diomedea exulans*). *Condor*, **86**, 182–186.
- Bryant, D.M. & Westerterp, K.R. (1980) The energy budget of the house martin (*Delichon urbica*). *Ardea*, **68**, 91–102.
- Buttner, W.A., Hayworth, A.M., Weathers, W.W. & Nagy, K.A. (1986) Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiological Zoology*, **59**, 131–149.
- Calow, P. (1979) The cost of reproduction – a physiological approach. *Biological Reviews*, **54**, 23–40.
- Chappell, M.A., Shoemaker, V.H., Janes, D.N., Bucher, T.L. & Maloney, S.K. (1993a) Diving behavior during foraging in breeding Adelie penguins. *Ecology*, **74**, 1204–1215.
- Chappell, M.A., Shoemaker, V.H., Janes, D.N., Maloney, S.K. & Bucher, T.L. (1993b) Energetics of foraging in breeding Adelie penguins. *Ecology*, **74**, 2450–2461.
- Clarke, A. & Prince, P.A. (1979) Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophrys* and *D. chrysostoma* at Bird Island. *Ibis*, **122**, 488–494.
- Costa, D.P. (1991) Reproductive and foraging energetics of high latitude penguins, albatrosses, and pinnipeds: implications for life history patterns. *American Zoologist*, **31**, 111–130.
- Costa, D.P. & Prince, P.A. (1987) Foraging energetics of Grey-headed Albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis*, **129**, 149–158.
- Croxall, J.P. & Prince, P.A. (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society*, **14**, 103–131.
- Croxall, J.P. & Prince, P.A. (1982) Calorific content of squid (Mollusca: Cephalopoda). *British Antarctic Survey Bulletin*, **55**, 27–31.
- Ellis, H.I. (1984) Energetics of free-ranging seabirds. *Seabird Energetics* (eds G.C. Whittow & H. Rahn), pp. 203–233. Plenum Press, New York.
- Flint, E.N. & Nagy, K.A. (1984) Flight energetics of free-living Sooty terns. *Auk*, **101**, 288–294.
- Furness, R.W. & Bryant, D.M. (1996) Effect of wind on field metabolic rates of breeding Northern Fulmars. *Ecology*, **77**, 1181–1188.
- Gabrielsen, G.W., Mehlum, F. & Nagy, K.A. (1987) Daily energy expenditure and energy utilization of free-ranging Black-legged kittiwakes. *Condor*, **89**, 126–132.
- Gales, R. (1989) Validation of the use of tritiated water, doubly labeled water, and <sup>22</sup>Na for estimating food, energy, and water intake in Little penguins, *Eudyptula minor*. *Physiological Zoology*, **62**, 147–169.
- Golet, G.H., Irons, D.B. & Costa, D.P. (2000) Energy costs of chick rearing in Black-legged kittiwakes (*Rissa tridactyla*). *Canadian Journal of Zoology*, **78**, 982–991.
- Jouventin, P. & Weimerskirch, H. (1990) Satellite tracking of wandering albatrosses. *Nature*, **343**, 746–748.
- Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Lasiewski, R.C. & Dawson, W.R. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*, **69**, 13–23.
- Lifson, N. & McClintock, R. (1966) Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology*, **12**, 46–74.
- Masman, D., Daan, S. & Dijkstra, C. (1988) Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *Journal of Animal Ecology*, **57**, 411–432.
- Nagy, K.A. (1980) CO<sub>2</sub> production in animals: analysis of potential errors in the doubly labeled water method. *American Journal of Physiology*, **238**, R466–R473.
- Nagy, K.A. (1983) The doubly labeled water (<sup>3</sup>HH<sup>18</sup>O) method: a guide to its use. Report No. 12–1417. University of California, Los Angeles, CA.
- Nagy, K.A. & Costa, D.P. (1980) Water flux in animals: analysis of potential errors in the tritiated water method. *American Journal of Physiology*, **238**, R454–R465.
- Nagy, K.A., Girard, I.A. & Brown, T.K. (1999) Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition*, **19**, 247–277.
- Nagy, K.A., Siegfried, W.R. & Wilson, R.P. (1984) Energy utilization by free-ranging Jackass penguins, *Spheniscus demersus*. *Ecology*, **65**, 1648–1655.
- Obst, B.S., Nagy, K.A. & Ricklefs, R.E. (1987) Energy utilization by Wilson's storm-petrel (*Oceanites oceanicus*). *Physiological Zoology*, **60**, 200–210.
- Ortiz, C.L., Costa, D.P. & Le Boeuf, B.J. (1978) Water and energy flux in elephant seal pups fasting under natural conditions. *Physiological Zoology*, **51**, 166–178.
- Pennycuik, C.J. (1982) The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Philosophical Transactions of the Royal Society of London B*, **300**, 75–106.
- Pennycuik, C.J. (1989) *Bird Flight Performance: a practical calculation manual*. Oxford University Press, Oxford.
- Prince, P.A., Wood, A.G., Barton, A.T. & Croxall, J.P. (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*, **4**, 31–36.
- Reyer, H.U. & Westerterp, K. (1985) Parental energy expenditure: a proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*). *Behavioral Ecology and Sociobiology*, **17**, 363–369.
- Ricklefs, R.E., Roby, D.D. & Williams, J.B. (1986) Daily energy expenditure by adult leach's storm-petrels during the nesting cycle. *Physiological Zoology*, **59**, 649–660.
- Shaffer, S.A. (2000) *Foraging ecology of Wandering Albatrosses (Diomedea exulans): impacts on reproduction and life history*. PhD Thesis. University of California, Santa Cruz, CA.
- Shaffer, S.A., Costa, D.P. & Weimerskirch, H. (in press) Comparison of methods to evaluate incubation energetics of wandering albatrosses. *Physiological and Biochemical Zoology*.
- Sibly, R.M. & Calow, P. (1986) *Physiological Ecology of Animals: an evolutionary approach*. Blackwell Scientific Publications, Oxford.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W.H. Freeman, New York, NY.
- Speakman, J.R. (1997) *Doubly Labeled Water: theory and practice*. Chapman & Hall, London.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Tickell, W.L.N. (1968) The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. *Antarctic Research Series*, **12**, 1–55.
- Walsberg, G.E. (1983) Avian ecological energetics. *Avian Biology* (eds D.S. Farner, J.R. King & K.C. Parkes), Vol. 7, pp. 161–220. Academic Press, New York, NY.
- Weimerskirch, H., Brothers, N. & Jouventin, P. (1997a) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with longline fisheries: conservation implications. *Biological Conservation*, **79**, 257–270.
- Weimerskirch, H., Doncaster, C.P. & Cuenot-Chaillet, F. (1994) Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London B*, **255**, 91–97.
- Weimerskirch, H., Fradet, G. & Cherel, Y. (1999) Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic prion. *Journal of Avian Biology*, **30**, 165–174.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D.P. (2000) Fast and fuel-efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B*, **267**, 1869–1874.

- Weimerskirch, H. & Jouventin, P. (1987) Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos*, **49**, 315–322.
- Weimerskirch, H., Lequette, B. & Jouventin, P. (1989) Development and maturation of plumage in the wandering albatross, *Diomedea exulans*. *Journal of Zoology, London*, **219**, 411–421.
- Weimerskirch, H., Mougey, T. & Hindermeyer, X. (1997b) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology*, **8**, 635–643.
- Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993) Foraging strategy of Wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325–342.
- Weimerskirch, H., Wilson, R.P. & Lys, P. (1997c) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series*, **151**, 245–254.
- Wilkinson, L. (1996) *SYSTAT 9.0 for Windows: statistics*. SPSS, Chicago, Illinois.
- Wilson, J.A. (1975) Sweeping flight and soaring by albatrosses. *Nature*, **257**, 307–308.
- Wilson, R.P., Weimerskirch, H. & Lys, P. (1995) A device for measuring seabird activity at sea. *Journal of Avian Biology*, **26**, 172–175.

Received 1 November 2000; revision received 13 June 2001