

The foraging behaviour and energetics of wandering albatrosses brooding chicks

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Abstract: The energy expenditure of ten (five male, five female) wandering albatrosses (*Diomedea exulans* Linnaeus 1758) brooding chicks on Bird Island, South Georgia, was measured using doubly-labelled water. At-sea foraging behaviour was measured in the same individuals using satellite telemetry and leg-mounted activity recorders. Mean mass-specific daily energy expenditure was 341 kJ kg⁻¹ day⁻¹ during a mean of 4.12 days at sea and did not differ between the sexes. This is significantly lower than previously reported for the species and the lowest recorded for any albatross. There were no significant relationships between energy expenditure and the proportion of time spent flying (59.7%), distance flown (1448 km) or average speed (16.5 km h⁻¹) suggesting that flying is not the most energetically expensive activity during foraging trips.

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Introduction

The behaviour of flighted pelagic seabirds at sea has traditionally been difficult to study because of their ability to cover great distances out of the range of both land- and ship-based observers. Recent advances in technology, however, have led to the miniaturization of a variety of devices for monitoring behaviour to the point where they can be deployed on, or in, medium to large seabirds without apparent adverse effects on their natural behaviour. This has enabled researchers to study various aspects of the physiology and behaviour of seabirds at sea, such as body temperature, heart rate, time spent flying, foraging times and locations, diving patterns and meal sizes in a range of species (e.g. Prince & Morgan 1987, Jouventin & Weimerskirch 1990, Weimerskirch & Wilson 1992, Afanasyev & Prince 1993, Bevan *et al.* 1994, 1995, Huin 1994, Prince *et al.* 1994, Falk & Moller 1995). Size constraints, however, still limit the number and type of devices that can be deployed and few studies have managed simultaneously to monitor more than one of these parameters; the energy costs of at-sea behaviour have been particularly neglected in recent studies.

The wandering albatross (*Diomedea exulans* Linnaeus 1758) is the largest and most pelagic of all seabirds. It breeds biennially on subantarctic islands throughout the Southern Ocean, a successful breeding season lasting nearly one year (Tickell 1968, Croxall *et al.* 1990). Several recent satellite tracking studies have revealed that wandering albatrosses have an extensive foraging range during the breeding season, travelling up to 15 000 km in a single foraging trip (Jouventin & Weimerskirch 1990, Prince *et al.* 1992, Weimerskirch *et al.* 1993). The monitoring of foraging times and meal sizes, using stomach temperature archival recorders (Weimerskirch & Wilson 1992, Wilson *et al.* 1995), has suggested that

wandering albatrosses capture the majority of their prey during the day when, as indicated by data from leg-mounted activity recorders, they spend as little as 17% of the time on the water (Prince & Morgan 1987). Weimerskirch & Wilson (1992) estimate that over 50% of prey items weigh less than 200 g (but see Wilson *et al.* 1995) and, by combining satellite tracking with stomach temperature recording, they suggested that wandering albatrosses encounter prey at a rate of one item for a minimum of every 107 km travelled. It is not surprising, therefore, that these birds may spend up to 74% of the time away from the nest flying (Afanasyev & Prince 1993).

The wandering albatross uses a “dynamic soaring” mode of flight (Pennycuik 1982) which provides a substantial energy-saving advantage over flapping flight (Baudinette & Schmidt-Nielsen 1974). It is the energy efficiency of soaring flight that enables wandering albatrosses to cover great oceanic distances during foraging trips with the lowest energy expenditure (1.83 times basal metabolic rate) recorded for any free-ranging bird (Adams *et al.* 1986). Although recent studies of at-sea behaviour have provided new insights into the foraging ecology of this species, no information is available on how different behaviours relate to energy expenditure. In the present study, our aim was to investigate the relationship between foraging range, activity patterns and energy expenditure.

Methods

The study was conducted on Bird Island, South Georgia (54°00'S, 38°02'W), during the 1992 chick-rearing period. The energy expenditure, at-sea activity and foraging range of adult wandering albatrosses were measured during the early

brood stage (March–April).

Energy expenditure

The energy expenditure of ten birds (five male, five female from separate nests) was determined using the doubly-labelled water method (Lifson & McClintock 1966, Nagy 1980, Speakman 1993). The energy expenditures of two individuals (one male, one female) were measured on two consecutive foraging trips.

After being weighed on a spring balance (± 0.1 kg), each individual was given an oral dose, by stomach tube, of 10 ml H_2^{18}O 10% AP (Isotec Inc., Miamisburg, OH, USA) and a 1 ml weighed dose (± 0.01 g) of tritiated water (HTO; $200 \mu\text{Ci ml}^{-1}$) by intra-muscular injection. Each bird was kept in a portable enclosure next to its nest for an isotope equilibration period of four hours. A blood sample (5 ml) was then collected from a tarsal vein into a heparinized syringe before the bird was released. The times of the bird's departure from, and return to, the colony were recorded by direct observation.

Upon return to the colony each bird was recaptured, before it relieved its mate from brooding duties, weighed and a final blood sample was collected to determine the clearance rates of the administered isotopes. In two individuals another blood sample was also collected after they returned from their next foraging trip. To minimize the handling time and the effects of stress, background blood samples were not collected from the study individuals. Instead, blood samples were collected from six control animals to determine the background levels of isotopes in the albatross population. All blood samples were stored at 4°C for several hours before being centrifuged and the plasma fraction separated. For HTO analysis, subsamples (1–2 ml) of plasma were stored frozen (-20°C) in plastic vials until analysed in November 1993. For H_2^{18}O analysis, aliquots (25–50 μl) of plasma were stored in flame-sealed capillary tubes until analysis in January 1994.

To measure the specific activity of tritium in plasma, samples were thawed and 0.2 ml subsamples were distilled into preweighed scintillation vials following the procedures of Ortiz *et al.* (1978). The vials were then reweighed to obtain the mass of the water sample, accurate to 0.1 mg. Scintillant (10 ml Ultima Gold; Canberra Packard, Brook House, Pangbourne, Berkshire, UK) was added to the vials which were then counted for 10 min in a Beckman LS1701 scintillation counter with correction for quenching by means of the sample channels ratio and an external standard to set the counting window for each vial. Samples were analysed in duplicate and each vial was counted twice. Subsamples (0.2 ml) of the injectant were counted in the same way, and at the same time, as the water from the plasma samples to determine the specific activity of the tritium injected.

Plasma samples were analysed for ^{18}O content at Centrum voor Isotopen Onderzoek, Gröningen, the Netherlands, following the methods of Masman (1986). Isotopic enrichments were determined in triplicate on a SIRA-9 mass

spectrometer. Because the H_2^{18}O was administered orally, we were not confident that the animals would receive an accurately measured dose and, hence, oxygen dilution space could not be determined. Total body water (TBW) was, therefore, calculated only from the initial dilution of HTO (Nagy 1983). Total body water at the end of the study period was calculated by multiplying the fractional water content at the beginning of the study by body mass upon recapture.

Carbon dioxide production was calculated from DLW measurements using the equations of Speakman *et al.* (1993) accounting for changes in TBW. A constant of 25.2 J ml^{-1} was used to convert CO_2 production to energy expenditure (Costa 1987) based on the average calorific value of chemical components of the diet (35% squid, 41.5% fish, 0.2% crustaceans and 18.8% carrion) of wandering albatross at Bird Island (Clarke & Prince 1979, Prince & Morgan 1987). Time ashore was calculated as the difference between the duration of the energy expenditure measurement and the time at sea (determined by direct observation). At-sea metabolic rate (MR, $\text{kJ kg}^{-1} \text{ day}^{-1}$) was then calculated for each animal by solving the equation: Measured MR = [(Ashore MR) (Proportion of time ashore)] + [(At-sea MR) (Proportion of time at sea)], assuming the metabolic rate while ashore to be $248 \text{ kJ kg}^{-1} \text{ day}^{-1}$, the rate reported for incubating wandering albatrosses (Brown & Adams 1984).

At-sea activity and foraging range

An activity recorder with a saltwater switch (24 g, 1.8 cm diameter tube of 8.2 cm length) was attached to a darvic ring on one of the legs of each bird (Afanasyev & Prince 1993). Whether the instrument was wet or dry was recorded at 3 s intervals and integrated hourly to give the proportion of every hour the bird spent flying or on the water. Night was defined as the dark period between the midpoints of civil twilight at South Georgia.

Information on foraging locations and range was obtained using satellite telemetry. Toyocom T2028C platform terminal transmitters (PTTs) weighing 180 g (1.3–2% of bird's body mass) were attached to the dorsal feathers of eight birds following the procedures detailed in Prince *et al.* (1992). Data on the position of instrumented birds were obtained via the ARGOS system and manipulated with purpose-built computer software. Only location estimates of ARGOS system Class = 0 (at least two transmitter messages received during the satellite pass) or better were used for mapping the general flight path of the bird's foraging trip whereas only Class 1–3 (accuracy of 100 m–1 km) were used for flight speed estimates (Prince *et al.* 1992). Both PTT and activity recorder were removed from the study animals at the end of the measurement intervals.

Statistical analyses followed methods outlined in Sokal & Rohlf (1981) and Zar (1984) using Unistat® Statistical Package (Version 4.5, Unistat Limited, London, UK). The Kolmogorov-Smirnov test was used to determine whether

Table I. Sex, measurement interval, body mass, total body water and CO₂ production rates of wandering albatrosses studied during the brood period.

Bird	Sex	Study period (days)	Body mass (kg)		TBW (kg)		TBW (%)	CO ₂ production (ml kg ⁻¹ min ⁻¹)
			initial	final	initial	final		
1	M	3.88	11.3	11.1	4.71	4.63	41.7	8.12
1	M	6.13	11.1	11.1	4.63	4.63	41.7	9.61
2	M	5.96	12.3	11.5	5.10	4.77	41.5	7.45
3	M	7.00	10.0	9.0	4.53	4.08	45.3	6.18
4	M	5.88	11.5	10.8	5.65	5.31	49.1	7.24
5	M	5.17	10.0	8.7	4.89	4.26	48.9	8.43
6	F	3.92	9.3	9.4	3.83	3.88	41.2	9.87
7	F	5.96	10.0	9.5	4.02	3.82	40.2	8.37
8	F	4.04	9.7	10.5	4.62	5.00	47.6	9.41
8	F	6.81	10.5	9.0	5.00	4.29	47.6	8.44
9	F	8.88	8.7	7.8	3.85	3.45	44.3	8.23
10	F	5.13	7.8	7.9	3.46	3.50	44.3	10.08
Mean		5.73	10.2	9.7	4.52	4.30	44.5	8.45
S.E.		0.40	0.4	0.4	0.17	0.16	0.9	0.32

data were normally distributed and an *F*-test was used to confirm homogeneity of variances. Unless otherwise stated, data are presented as means \pm 1 s.e. and results were considered to be significant at the $P < 0.05$ level.

Results

The measurement interval, sex, body mass, TBW, and CO₂ production rates for the ten study birds are presented in Table I. Males were significantly heavier (10.7 ± 0.4 kg) and had larger TBW pools (4.9 ± 0.2 kg) than females (mass 9.2 ± 0.3 kg, TBW 4.1 ± 0.2 kg; $P < 0.02$ in both cases) but percent TBW ($44.5 \pm 0.9\%$) was not significantly different between the sexes ($P > 0.7$). Mass-specific CO₂ production rates during the whole of the measurement period were significantly greater in females (9.1 ± 0.3 ml min⁻¹ kg⁻¹) than in males (7.8

± 0.4 ml min⁻¹ kg⁻¹; $t_{10,0.05} = 2.30$, $P < 0.05$). At-sea mass-specific CO₂ production rates did not differ significantly between the sexes (females 10.5 ± 1.0 ml min⁻¹ kg⁻¹, males 8.3 ± 0.6 ml min⁻¹ kg⁻¹; $t_{10,0.05} = 1.87$, $P > 0.09$, combined 9.4 ± 0.7 ml min⁻¹ kg⁻¹). However, as no sex-specific on-land CO₂ production rates could be assigned to these birds, the lack of statistical difference in at-sea CO₂ production rates should be viewed with caution. Indeed, one could probably infer that even at the $P = 0.09$ level there may well have been a significant difference given a larger sample size. For the purposes of the remaining analyses in this study, however, we have assumed at-sea mass-specific CO₂ production rates are the same for each sex.

Due to instrument failure, data on at-sea activity and foraging range were each obtained for only eight foraging trips. These data and the duration of each foraging trip, daily

Table II. Time at sea, experimental protocol, mass change, energy expenditure, at-sea activity and distance flown by wandering albatrosses making foraging trips during the brood period.

Bird	Time at sea (days)	Type of trip ¹	Instruments carried ²	Mass change (kg day ⁻¹)	Energy expenditure at sea ³ (kJ day ⁻¹)	Multiples of BMR ⁴ (kJ kg ⁻¹ day ⁻¹)	% of time flying	Distance flown (km)	Average speed (km h ⁻¹)	
1	2.17	shelfedge	AR, PTT	-0.05	3696	330	1.53	57.9	732	13.2
1	4.17	polar front	AR, PTT	0.00	4398	396	1.83	92.8	1941	28.1
2	5.00	*	AR, PTT	-0.13	3248	273	1.26	*	1687	14.5
3	6.08	polar front	AR, PTT	-0.14	2079	219	1.01	28.3	1869	10.9
4	3.17	*	AR, PTT	-0.12	2998	269	1.24	57.4	*	*
5	3.71	*	AR, PTT	-0.25	3007	322	1.49	*	*	*
6	3.71	shelfedge	AR, PTT	0.03	3407	364	1.69	*	722	10.0
7	4.50	*	AR	-0.08	3117	320	1.48	52.5	*	*
8	1.29	shelfedge	AR, PTT	0.20	5668	561	2.60	65.2	426	29.5
8	3.81	polar front	AR, PTT	-0.22	3287	337	1.56	69.4	2688	13.1
9	7.63	*	AR	-0.10	2514	305	1.41	*	*	*
10	4.19	polar front	AR, PTT	0.02	3080	392	1.82	54.2	1282	12.7
Mean	4.12			-0.07	3375	341	1.58	59.7	1418	16.5
S.E.	0.46			0.03	254	24	0.10	4.4	187	2.6

¹Foraging trips fell into two broad categories: to the continental shelf edge (short) and the Antarctic Polar Frontal Zone (long); ²AR = activity recorder and PTT = satellite transmitter. Instrument failure prevented data collection from some animals and this is indicated by an * in the table; ³Calculated from CO₂ production rates using a conversion of 25.2 kJ per litre of CO₂; ⁴BMR = 216 kJ kg⁻¹ day⁻¹ (Brown & Adams 1984).

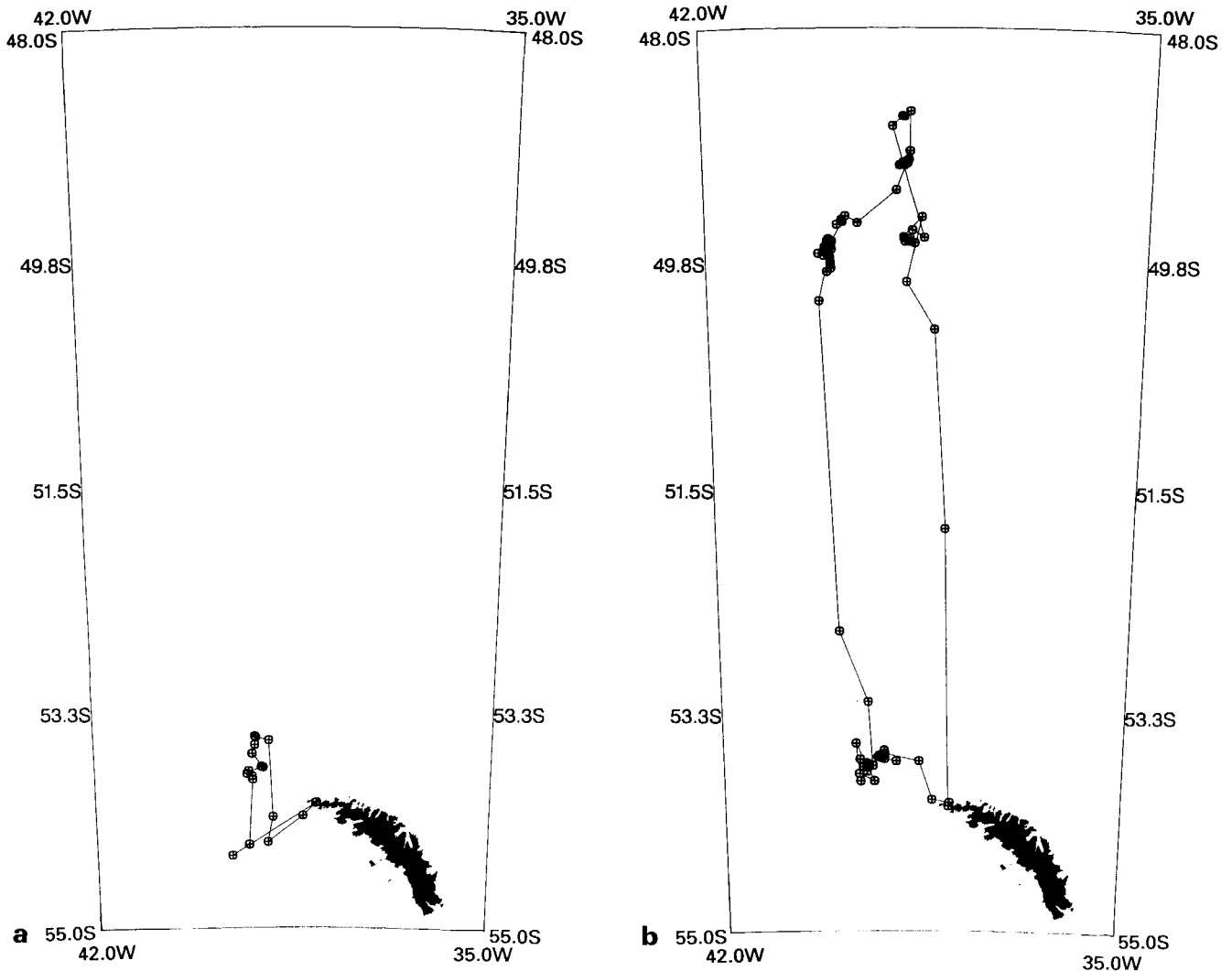


Fig. 1. Examples of the two distinct types of foraging trips observed in this study: **a.** short trips to the continental shelf edge; and **b.** longer trips to the Antarctic Polar Frontal Zone, shown here for Bird 8 (first trip) and Bird 3, respectively.

mass change, and energy expenditure are presented in Table II. There were no significant differences in the time spent at sea (4.12 ± 0.46 days), proportion of time spent flying ($59.7 \pm 4.9\%$), distance flown (1448 ± 211 km), daily mass change (-0.07 ± 0.03 kg \cdot day $^{-1}$) or at-sea metabolic rate (340.7 ± 23.8 kJ \cdot kg $^{-1}$ \cdot day $^{-1}$) between the sexes ($P > 0.1$ in all cases) so the data were combined. Activity patterns differed temporally with birds spending $71.5 \pm 4.1\%$ of daylight time flying compared to only $44.0 \pm 9.0\%$ during the night.

There were generally two types of foraging trips undertaken by the study birds: short trips ranging no further than the continental shelf edge; and longer trips ranging much further to the Antarctic Polar Frontal Zone. Examples of the track typical of such foraging trips is given in Fig. 1; the appropriate categories for each bird are listed in Table II.

Both absolute and mass-specific daily energy expenditure were not related to the proportion of time spent flying, the distance flown, or average speed ($P > 0.2$ in all cases).

Furthermore, there were no apparent relationships between these variables and the type of foraging trip undertaken (shelf edge or polar front). Mass-specific daily energy expenditure was, however, positively correlated with daily mass gain ($r^2 = 0.63$, $n = 12$, $P < 0.002$; Fig. 2a) and negatively correlated with time at sea ($r^2 = 0.37$, $n = 12$, $P < 0.04$, Fig. 2b). Daily mass gain was not related to either time at sea, the proportion of time spent flying, the distance flown or the average speed during a foraging trip ($P > 0.2$ in all cases). Absolute mass gain, however, was significantly negatively correlated with time at sea ($r^2 = 0.35$, $n = 12$, $P < 0.05$).

Discussion

Body composition and energy expenditure

The body masses of both the male and female wandering albatrosses recorded in the present study are similar to those

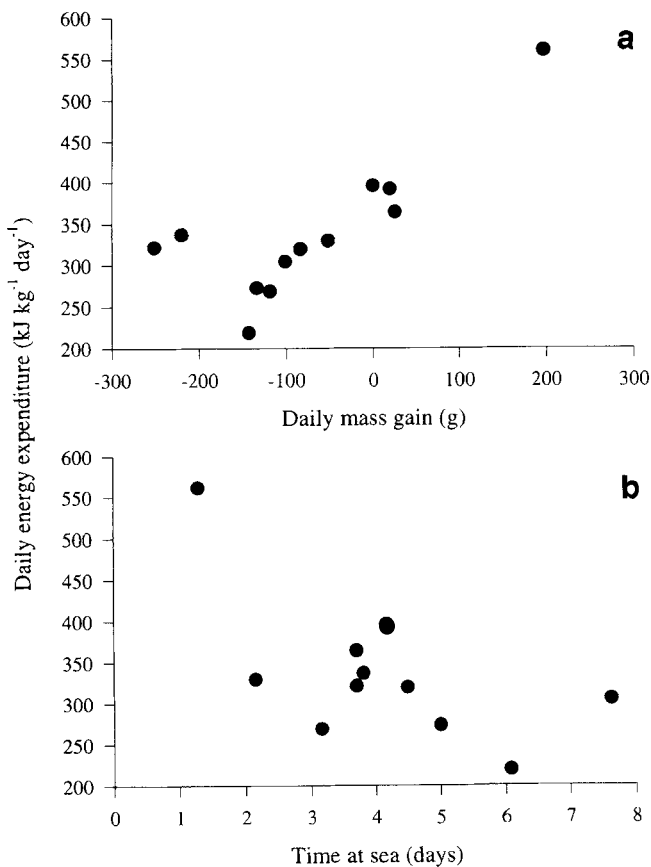


Fig. 2. a. The relationship between daily energy expenditure and daily mass gain during time at sea; and b. the relationship between daily energy expenditure and time at sea in wandering albatrosses during the brood period.

previously reported for this species at South Georgia (Croxall & Ricketts 1983) and, as in all albatross species, the males were heavier than the females (Warham 1990). The mean percent TBW of 44.5% found in this study is similar to the 47.5% reported by Adams *et al.* (1986) for wandering albatrosses breeding on Marion Island. Such TBW contents are lower than that reported for many marine and aquatic birds (Mahoney & Jehl 1984) but similar to that found in other procellariiforms (e.g. 45.9% in Wilson's storm petrel *Oceanites oceanicus* Kuhl 1820 and 51.9% in southern giant

petrels *Macronectes giganteus* Gmelin 1789) (B.S. Obst, K.A. Nagy & R.E. Ricklefs unpublished data in Adams *et al.* 1986), including the Laysan albatross (*D. immutabilis* Rothschild 1893, 47%) (Pettit *et al.* 1988). It is thought this is due to the relatively long wings and flight feathers in procellariiforms contributing relatively more dry matter to the total body mass than in other species (Adams *et al.* 1986). In contrast, however, Costa & Prince (1987) recorded relatively high TBWs of 57.9% in the grey-headed albatross (*D. chrysostoma* Forster 1785).

The greater mass-specific CO₂ production rates, and hence metabolic rates, in females than in males found in the present study may simply reflect their smaller size (greater surface area to volume ratio). However, they may also reflect differences in activity levels. Whereas our methods were not able to document a significant difference in at-sea metabolic rates between the sexes, more detailed analyses of both on-land and at-sea activity patterns and their energetic costs may provide a better understanding of the observed sex-specific difference in CO₂ production rates.

The mean at-sea mass-specific energy expenditure recorded in the present study (341 kJ kg⁻¹ day⁻¹) is significantly lower ($t_{19,0.05} = 6.05, P < 0.0001$) than that reported by Adams *et al.* (1986) for wandering albatrosses at Marion Island with 40–80 day old chicks (397 kJ kg⁻¹ day⁻¹). This is due to differences in the equations used for calculating carbon dioxide production from isotope dilution and clearance rates. In the present study we used equations based on the two pool model (Speakman *et al.* 1993) whereas Adams *et al.* (1986) used equations for the single pool model (Lifson & McClintock 1966). The two pool model invariably produces an estimate lower than the single pool model and, indeed, the difference between the results of present study and that of Adams *et al.* (1986) disappears when the Lifson & McClintock (1966) equations are applied to our data (395 kJ kg⁻¹ day⁻¹; $t_{19,0.05} = 0.149, P > 0.88$). Recent evidence in birds suggests the two pool model may be the most appropriate (Bevan *et al.* 1995) and, hence, for this reason we have presented our results using equations based on it. Nonetheless, the mass-specific energy expenditures reported in both studies are considerably lower than that observed in other species of albatross (Table III).

The grey-headed albatross, Laysan albatross and white-

Table III. Comparison of at-sea mass-specific energy expenditure in four species of albatross.

Species	Mass (kg)	At-sea energy expenditure (kJ kg ⁻¹ day ⁻¹)	Multiples of BMR	Stage of breeding season	Reference
Wandering albatross <i>D. exulans</i>	9.95	341	1.58*	brood period	This study
	8.42	397	1.83*	chick alone	Adams <i>et al.</i> (1986)
Grey-headed albatross <i>D. chrysostoma</i>	3.66	657	2.47*	incubation period	Costa & Prince (1987)
Laysan albatross <i>D. immutabilis</i>	3.06	676	2.60*	incubation period	Pettit <i>et al.</i> (1988)
White-capped albatross <i>D. cauta cauta</i>	3.92-4.2	670	2.57-2.62*	chick alone	Green & Brothers (1995)

*Measured basal metabolic rate (see Table II); *BMR predicted using $BMR = 381.8 M^{0.721}$ where BMR is in kJ day⁻¹ and M is body mass in kg (Ellis 1984).

capped albatross (*D. cauta cauta* Gould 1841) all expend energy at 2.4–2.6 times basal metabolic rate while foraging whereas on average wandering albatrosses only expend energy at 1.58–1.83 times BMR (Adams *et al.* 1986, Costa & Prince 1987, Pettit *et al.* 1988, Green & Brothers 1995). All albatrosses are anatomically adapted for soaring flight (Pennycuik 1982) but there are no data available on energy expenditure during flight in any of these species to compare the cost of flying. Adams *et al.* (1986) suggested that the higher energetic cost of foraging in the grey-headed albatross compared to that in the wandering albatross may be partially due to differences in the amount of time spent flying between the two species. However, reports on the proportion of foraging trips spent flying vary considerably within species (Prince & Morgan 1987, Afanasyev & Prince 1993, this study) making it difficult to infer such time-energy budget differences between species. More recently, Prince *et al.* (1994) have observed that mollymawks submerge to much greater depths (2.5–4.7 m) than does the wandering albatross (0.3 m) and suggested that diving behaviour may be a typical part of foraging activity in mollymawks. Foot propelled diving is energetically expensive (Ellis 1984) and this activity may explain the higher foraging energy expenditure of mollymawks compared to wandering albatrosses.

At-sea behaviour

The mean time at sea observed in the present study (4.12 days) is longer than the previously reported means during the brood period for this species at South Georgia and Iles Crozet (2.7 and 2.8 days, respectively) but well within the ranges (1–10 days and 1.3–5 days, respectively; Tickell 1968, Weimerskirch *et al.* 1993). The range of trip durations in this study was also considerable (1.3–7.6 days). Due to small sample sizes, we were not able to assess the effect of instrumentation on foraging trip BMR. However, Weimerskirch *et al.* (1992) found no difference in the time spent at sea between birds instrumented with a PTT and controls.

Foraging trip durations of wandering albatrosses vary considerably throughout the breeding cycle (Tickell 1968, Weimerskirch *et al.* 1993). In a study of breeding birds at Iles Crozet, Weimerskirch *et al.* (1993) have shown that these changes are associated with changes in foraging ranges; birds at sea for short periods (2.4–2.8 days) forage within 260 km of the colony and travel distances of less than 1000 km whereas birds at sea for long periods (>10 days) forage up to 1500 km from the island and may travel as much as 6000 km. Similarly, South Georgia birds in the late chick-rearing period (August) travel up to 5000 km during mean foraging trip durations of seven days (Prince *et al.* 1992) whereas during the brood period (this study) birds travel less than 1500 km during short trips.

In the present study there was no relationship between the distance covered during a foraging trip and the time spent at

sea. Similarly, whereas Weimerskirch *et al.* (1993) found a positive relationship between time at sea and distance covered during long trips of the incubation and chick-rearing periods, they found no such relationship during the brood period. The average flight speed (16.5 km h⁻¹) recorded in this study is approximately half that observed by Prince *et al.* (1992) for South Georgia birds during the chick rearing period (29 km h⁻¹) but similar to the 16 km h⁻¹ reported for wandering albatrosses at the Auckland Islands during the incubation period (Walker *et al.* 1995). Whether these differences in flight speeds are due to differences in foraging effort or prevailing weather patterns is not known.

The proportion of time spent flying varied substantially between birds (range: 28–93%) but the mean (60%) fell within the range of means previously reported for the species (57–74%, Prince & Morgan 1987, Afanasyev & Prince 1993). The temporal distribution of the time spent flying concurs with Afanasyev & Prince's (1993) previous observation that most of the flying is done during the daylight hours. These results, in conjunction with information from stomach temperature loggers on the timing of foraging and satellite tracking, support Weimerskirch & Wilson's (1992) contention that wandering albatrosses generally rest during periods of darkness but actively search for food during the day.

Energetic costs of foraging

There were no relationships between at-sea energy expenditure and distance flown, the average speed or proportion of time spent flying. This suggests that, in general, flying is not the most energy expensive activity during foraging trips and is consistent with dynamic soaring being an energy efficient mode of flight (Baudinette & Schmidt-Nielsen 1974). Indeed, satellite tracking studies have shown that the flight paths of wandering albatrosses generally make use of prevailing winds, flying constantly with a crosswind in the hindquarter (Weimerskirch *et al.* 1992). At-sea daily energy expenditure was, however, negatively related to the time spent at sea. One possible explanation for this observation is that on longer foraging trips a smaller proportion of the overall time is spent in certain activities which may be energetically expensive. For example, birds that make long trips may spend most of the time in transit to the foraging area (Prince *et al.* 1992). During transit flight, birds may make use of the prevailing winds to reduce energy expenditure but manoeuvring within the foraging zone in search of food may require flying in many different directions over short distances, resulting in considerably greater energy expenditure. Investigations of energy expenditure with finer temporal resolution and on an activity-specific basis, as is now possible with the recent advances in heart-rate monitoring (Bevan *et al.* 1994, 1995), are needed to verify this hypothesis.

Daily mass gain was positively correlated with at-sea daily energy expenditure. This suggests that birds expending

more energy in search of food are more successful foragers. Interestingly, the amount of mass gained during a foraging trip was negatively related to the time spent at sea. This is the opposite to what has been observed in wandering albatrosses during the incubation period at the Iles Crozet (Weimerskirch 1995).

In summary, the results of the present study further illustrate the energetic efficiency of flight in wandering albatrosses. The absence of any relationship between foraging behaviour and energy expenditure is consistent with the current interpretation of the foraging strategy in this species; using the prevailing weather conditions to cover great distances in search of food to scavenge (Prince *et al.* 1994). It would be of great interest, therefore, to conduct similar investigations on mollymawks, which have a similar mode of flight but a different feeding behaviour of greater potential energetic cost (Ellis 1984, Prince *et al.* 1994).

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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.
- AFANASYEV, V. & PRINCE, P.A. 1993. A miniature storing activity recorder for seabird species. *Ornis Scandinavica*, **24**, 243-246.
- BAUDINETTE, R.V. & SCHMIDT-NIELSEN, K. 1974. Energy cost of gliding flight in herring gulls. *Nature*, **248**, 83-84.
- 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*, **B350**, 119-131.
- BEVAN, R.M., WOAKES, A.J., BUTLER, P.J. & BOYD, I.L. 1994. The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatross *Diomedea melanophrys*. *Journal of Experimental Biology*, **193**, 119-137.
- 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.
- CLARKE, A. & PRINCE, P.A. 1979. Chemical composition and calorific value of food fed to mollymawk chicks *Diomedea melanophrys* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis*, **122**, 488-494.
- COSTA, D.P. 1987. Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. In HUNTLEY, A.C., COSTA, D.P., WORTHY, G.A.J. & CASTELLINI, M.A., eds. *Approaches to marine mammal energetics*. Lawrence, Kansas: Allen Press, 43-66.
- COSTA, D.P. & PRINCE, P.A. 1987. Foraging energetics of Grey-headed Albatross *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis*, **129**, 149-158.
- CROXALL, J.P. & RICKETTS, C. 1983. Energy costs of incubation in the wandering albatross *Diomedea exulans*. *Ibis*, **125**, 33-39.
- CROXALL, J.P., ROTHERY, P., PICKERING, S.P.C. & PRINCE, P.A. 1990. Reproductive performance, recruitment and survival of wandering albatross *Diomedea exulans* at Bird Island, South Georgia. *Journal of Animal Ecology*, **59**, 773-794.
- ELLIS, H.I. 1984. Energetics of free-ranging seabirds. In WHITTOW, G.C. & RAHN, H., eds. *Seabird energetics*. New York: Plenum Publishing, 203-234.
- FALK, K. & MOLLER, S. 1995. Satellite tracking of high-arctic northern fulmars. *Polar Biology*, **15**, 495-502.
- GREEN, B. & BROTHERS, N. 1995. Field energetics of white-capped albatross, *Diomedea cauta cauta* and growth of chicks. *Abstracts of the First International Conference on the Biology and Conservation of Albatrosses 28 August-1 September 1995, Hobart, Australia*, 17.
- HUIN, N. 1994. Diving depths of white-chinned petrels. *Condor*, **96**, 1111-1113.
- JOUVENTIN, P. & WEIMERSKIRCH, H. 1990. Satellite tracking of wandering albatross. *Nature*, **343**, 746-748.
- LIFSON, N. & MCCLINTOCK, R. 1966. Theory and use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology*, **12**, 46-74.
- MAHONEY, S.A. & JEHL, J.R. 1984. Body water content in marine birds. *Condor*, **86**, 208-209.
- MASMAN, D. 1986. *The annual cycle of the kestrel Falco tinnunculus: a study in behavioural energetics*. Ph.D. thesis, University of Gröningen, [Unpublished.]
- NAGY, K.A. 1980. CO₂ production in animals: an analysis of potential errors in the doubly-labelled water method. *American Journal of Physiology*, **238**, R466-R473.
- NAGY, K. 1983. *The doubly-labelled water (³H¹⁸O) method: a guide to its use*. UCLA Publication 12-1417, 45 pp.
- ORTIZ, C.L., COSTA, D.P. & LEBOEUF, B.J. 1978. Water and energy flux in elephant seal pups fasting under natural conditions. *Physiological Zoology*, **51**, 166-178.
- PENNYCUICK, 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*, **B300**, 75-106.
- PETTIT, T.N., NAGY, K.A., ELLIS, H.I. & WHITTOW, G.C. 1988. Incubation energetics of the Laysan albatross. *Oecologia*, **74**, 546-550.
- PRINCE, P.A., HUIN, N. & WEIMERSKIRCH, H. 1994. Diving depths of albatrosses. *Antarctic Science*, **6**, 353-354.
- PRINCE, P.A. & MORGAN, R.A. 1987. Diet and feeding ecology of Procellariiformes. In CROXALL, J.P., ed. *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge: Cambridge University Press, 135-171.
- PRINCE, P.A., WOOD, A.G., BARTON, T. & CROXALL, J.P. 1992. Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*, **4**, 31-36.
- SOKAL, R.R. & ROHLF, F.J. 1981. *Biometry: the principles and practice of statistics in biological research*. 2nd ed. San Francisco: W.H. Freeman and Company, 859 pp.
- SPEAKMAN, J.R. 1993. How should we calculate CO₂ production in doubly-labelled water studies of animals? *Functional Ecology*, **7**, 746-750.
- SPEAKMAN, J.R., NAIR, K.S. & GORAN, M.I. 1993. Revised equations for calculating CO₂ production from doubly-labelled water in humans. *American Journal of Physiology*, **264**, E912-E917.
- TICKELL, W.L.N. 1968. The biology of the great albatrosses *Diomedea exulans* and *D. epomophora*. *Antarctic Research Series*, **12**, 1-55.
- WARHAM, J. 1990. *The petrels: their ecology and breeding systems*. San Diego: Academic Press, 440 pp.
- WALKER, K.A., ELLIOT, G., NICHOLLS, D.G., MURRAY, M.D. & DILKS, P. 1995. Satellite tracking of Wandering Albatross (*Diomedea exulans*) from the Auckland Islands: preliminary results. *Notornis*, **42**, 127-135.
- WEIMERSKIRCH, H. 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia*, **102**, 37-43.
- WEIMERSKIRCH, H., SALAMOLARD, M. & JOUVENTIN, P. 1992. Satellite

- telemetry of foraging movements in the wandering albatross. In FRIEDE, I.G. & SWIFT, S.M., eds. *Wildlife telemetry*. Chichester: Ellis Harwood, 185-198.
- 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. 1992. When do wandering albatross *Diomedea exulans* forage? *Marine Ecology Progress Series*, **86**, 297-300.
- WILSON, R.P., PUTZ, K., GREMILLET, D., CULIK, B.M., KIERSPEL, M., REGEL, J., BOST, C.A., LAGE, J. & COOPER, J. 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology*, **198**, 1115-1135.
- ZAR, J.H. 1984. *Biostatistical analysis*. 2nd ed. Englewood Cliffs, NJ: Prentice-Hall Inc., 718 pp.