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The energy expenditure of free-ranging black-browed albatrosses

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SUMMARY

As heart rate (f_H) can be used to determine the energy expenditure of black-browed albatrosses (*Diomedea melanophrys*) (Bevan *et al.* 1994), data loggers – recording f_H and abdominal temperature (T_{ab}) – were implanted into free-ranging black-browed albatrosses breeding at South Georgia. Five birds also had salt water switches (sws) attached to one leg to record when the birds were on the water, and two others had satellite transmitters attached to their back to determine the birds' position at sea. The birds were released into their natural environment and recaptured, on average, 23 days later when the data loggers were removed. The f_H data were then converted into estimates of energy expenditure (EE) using a previously derived equation.

The mean EE during incubation and brooding were 2.22 and 2.42 W kg⁻¹, respectively. When the birds were foraging at sea, EE increased to between 4.63 and 5.80 W kg⁻¹, depending on the phase of the reproductive cycle. As the birds spent approximately the same length of time at the nest and at sea during incubation and brooding, the overall mean EE during these phases were 3.63 and 3.54 W kg⁻¹ respectively. These rates are significantly lower than that during the chick-rearing phase when a high level of foraging EE is maintained almost continuously.

By combining information from the sws with the f_H data, it was possible to determine the EE of the birds when on the water (5.77 W kg⁻¹) and when flying (6.21 W kg⁻¹). These values are approximately twice the estimated basal metabolic rate (BMR) for the species. The energy costs of flight are half previous values, estimated using the doubly labelled water technique, because of the previous assumption that birds on the water have an EE equivalent to BMR.

When the birds were on the nest, T_{ab} was 39.3 ± 0.4 °C and this changed very little with time. However, when they were at sea, T_{ab} showed large variations, depending on the behaviour of the bird. Information from the sws indicated that all large drops (> 0.5 °C) in T_{ab} occurred when the birds were on water. The mean minimum value reached was 32.5 ± 2.0 °C. It is likely that ingestion of prey or water are the major causes of this decrease.

This is the first study to have used f_H extensively to determine the EE of a free-ranging marine bird. The advantages of using this technique are that data can be obtained over long durations with high resolution, permitting the EE of different activities to be estimated.

1. INTRODUCTION

A detailed knowledge of the energy expenditure (EE) of pelagic sea-birds is an essential component in our understanding of the foraging ecology of these animals and of their role in the nutrient fluxes within marine systems. However, because these birds forage at sea it is impossible to observe their behaviour continuously to determine activity and energy budgets. Although several recent studies have used satellite telemetry to determine the movements of some avian species at sea (Jouventin & Weimerskirch 1990; Prince *et al.* 1992; Weimerskirch *et al.* 1993; Salamolard & Weimerskirch 1993; Weimerskirch & Robertson 1994), such data are of limited use in estimating energy budgets because they provide little information on the actual behaviour of the bird.

The only technique, to date, that has been used extensively to determine the energy budgets of pelagic sea-birds is doubly labelled water (DLW) (Adams *et al.* 1986; Costa & Prince 1987; Obst *et al.* 1987; Birt-Friesen *et al.* 1989; Davis *et al.* 1989; Nagy *et al.* 1993). The method has its limitations, though, as the period of monitoring is restricted to a few days and its use is therefore restricted to specific periods of the reproductive cycle (Costa & Prince 1987). Probably its biggest drawback, however, is that it provides only a single value of EE over the entire monitoring period (for a review of the technique see Tatner & Bryant 1989). A number of studies have tried to circumvent these problems by dividing the monitoring period into time spent at sea and time spent at the nest in order to partition the energy usage (Adams *et al.* 1986; Davis *et al.* 1989; Kooyman *et al.* 1992). Other studies have

used the proportion of time a bird spends on the water (Prince & Francis 1984) to determine the costs of specific behaviours such as flight (Adams *et al.* 1986; Costa & Prince 1987). However, to understand fully the complexities of the energy budgets of pelagic seabirds, a method is required that can both measure the EE over long time periods and be used at a much finer time resolution.

Heart rate (f_H) has been shown to be at least as good an indicator of the metabolic rate (EE) as DLW in a number of species (Nolet *et al.* 1992; Bevan *et al.* 1994; Bevan *et al.* 1995). Coupled with this are recent technical advances that have enabled f_H to be recorded continuously in free-ranging animals using implanted heart rate data loggers (HRDL) (Woakes *et al.* 1995). These HRDL not only record f_H and temperature for long periods of time (> 30 days) but also have a time resolution as short as 15 s. A further advantage of using f_H is that physiological information can also be obtained e.g. the cardiac responses to different behaviours.

The black-browed albatross has been extensively studied over many years at Bird Island, South Georgia, and there is a wealth of information on its reproductive biology and ecology (Tickell & Pinder 1975; Prince 1980; Prince *et al.* 1994). The aims of the present study were to record f_H and abdominal temperature (T_{ab}) in free-ranging black-browed albatrosses, to monitor their behaviour and movements (in conjunction with other recording/transmitting devices) and to relate this behavioural information to the EE of the birds estimated from the f_H data (Bevan *et al.* 1994).

2. METHODS

(a) *Study animals*

Experiments were performed on black-browed albatrosses at colonies on Bird Island, South Georgia (54° S, 38° W) during the austral summers of 1991–92 and 1992–93. The study period covered the incubation, brooding and early to mid chick-rearing phases of the reproductive cycle. A total of 25 birds were used, 12 in 1991–92 and 13 in 1992–93.

(b) *Heart rate and temperature data-loggers*

Heart rate and T_{ab} were recorded in free-ranging birds using an implanted HRDL (Woakes *et al.* 1995). The HRDL monitors the electrocardiogram (ECG) of an animal and recognizes the QRS wave of each cardiac contraction. Temperature is recorded via a thermistor in the body of the HRDL and monitors the temperature at its position. In the present study, the HRDL were programmed to store the number of heart beats in each 30 s period, and to record the instantaneous temperature every 60 s. Programming the HRDL was achieved with a purpose-built interface unit connected, via an A/D converter card (PCL-711, PC-Labcard), to a laptop computer (Dell 316LT). The HRDL were prepared for implantation by first immersing them in paraffin wax and then coating the devices with silicone rubber. Before implantation, the HRDL were sterilized

in 90% alcohol. To download the data, the HRDL was removed from the bird, the silicone and wax coatings were removed and the HRDL connected to the interface unit and computer. A computer program downloaded the data to hard disk for later analysis.

Retrieved HRDL were, after downloading the data, reprogrammed and re-encapsulated. They were then immersed in a temperature bath and the temperature varied between 25 °C and 40 °C. The HRDL were held at each temperature for at least 15 min to ensure that the temperature of the HRDL had equilibrated with that of the water. At the end of the calibration, the HRDL was plunged into cold water, at approximately 20 °C, to measure the response time. The data were then downloaded to obtain the calibration. The HRDL took 440 ± 67 s to respond to a 21.2 ± 1.0 °C drop in temperature, and 229 ± 15 s to record a 90% change.

(c) *Implantation procedure*

Adult birds (25) of indeterminate sex were caught at the nest and transported back to the base. The implantation procedure was basically the same as that used to implant ECG transmitters (Stephenson *et al.* 1986). Briefly, the birds were anaesthetized with a halothane enriched air/O₂ mixture (halothane induction 1.5–2%, maintenance 0.75–1%; air:O₂ = 4:2) flowing into a mask at 6 l min⁻¹. Povidine was used to disinfect the incision area and the surrounding feathers. The sterilized HRDL was implanted into the abdominal cavity via a mid-line incision made in the skin and body wall muscle in the brood patch. A suture thread (Supramid) tied around the body of the HRDL was used to anchor it in place slightly forward of the incision area. Vicryl (Ethicon Ltd) was used to suture the body wall muscle and Supramid was used to suture the skin. An antibiotic powder was dusted onto the wound area, and a long acting antibiotic injected intramuscularly (Terramycin LA, Pfizer). Aseptic conditions were maintained wherever possible. The time at which the HRDL was implanted was noted to the nearest second. On recapture of the animal after 13–33 days, the HRDL was removed using the same procedure as during implantation, with the time of removal again being noted. The precise times of implanting and removal were used to synchronize the data downloaded from the HRDL. All birds were weighed on capture using a bag and spring balance (10 ± 0.1 kg Pesola).

When the birds were incubating, their egg was placed under a neighbouring bird until the implanted adult was returned to the nest. If brooding, the chick was also transported back to the base in an insulated box and kept warm until the adult bird was again released. It took approximately 2 h from capturing a bird to releasing it. A further seven birds were implanted at a hide overlooking one of the colonies, using the same procedure as outlined above, to minimize the time the birds spent away from the nest.

The birds were returned to the nest after the implantation procedure and replaced on their egg or chick. Nearly all birds immediately recommenced incubating or brooding, however a small number left the nest and had to be coaxed back. Of all the birds

implanted, only one deserted immediately and was not recaptured until the next season. Two other birds also deserted, one of them a day after implantation and the other after a rock fall destroyed its nest; both birds were recaptured. All nests were monitored daily to determine the presence of the experimental birds. After retrieval of the HRDL, the birds were again replaced at the nest and their nest attendance monitored.

(d) Salt-water switches

Five of the implanted birds were also equipped with salt-water switches (sws) (Afanasyev & Prince 1993) during the brooding period. The devices (mass = 24 g) were attached to a Darvic ring placed around the leg and measured the conductivity between two electrodes and therefore recorded the time spent on or off the sea. The devices sampled every 3 s and were programmed to record the proportion of the time that they had been in contact with seawater over each 12 min period of deployment. They were attached to birds between 6 and 12 days after implantation of the HRDL (and after the birds had been on the nest for at least 24 h) and were removed 3–7 days later. The sws were interrogated by a laptop computer and the stored data downloaded to disk for later analysis. The data were later reformatted so that they could be displayed and analysed with the f_H data.

(e) Satellite transmitters

Two of the implanted birds were also equipped with satellite transmitters (Microwave Telemetry Inc.; satellite transmitters (PTR) mass = 65 g) during the chick-rearing phase. The transmitters were attached as described in Prince *et al.* (1992) for the wandering albatross. Unlike the sws, the satellite transmitters were attached when the birds were still anaesthetised following implantation of the HRDL. This meant that the birds were only caught for the deployment and retrieval of the HRDL. Both birds were also equipped with a radio transmitter attached to a leg, the signals from which were continuously monitored so that the presence of the birds in the colony (and hence when the chicks were fed) could be noted. The two birds were tracked for 20 and 28 days.

(f) Data analysis

The data were displayed and analysed using purpose-written computer programs. Further analyses were performed with the statistical package SYSTAT (Systat Inc.). Data from the first two days after implantation were not analysed, to eliminate any effect of the operating procedure. Visual inspection of the data indicated that all birds had recovered within this period, with most appearing to have recovered within 24 h of the procedure. A Student's *t*-test on the data confirmed that there was no significant difference between the f_H of birds at the nest (incubating or brooding) two days after the implantation procedures and at the end of the recording period. Data could not

be analysed in a similar fashion for the chick rearing phases as the birds spent too little time at the nest, but it was assumed that the recovery period would be the same.

The f_H data were used to estimate EE using the relation between f_H and oxygen consumption (\dot{V}_{O_2}) obtained from black-browed albatrosses walking on a treadmill (Bevan *et al.* 1994):

$$\dot{V}_{O_2} = 0.0158f_H^{1.60}, r^2 = 0.85 \quad (1)$$

where \dot{V}_{O_2} is in ml min⁻¹, and f_H is in beats min⁻¹. As the measured body mass of the free-ranging albatrosses can vary substantially due to varying amounts of food carried in the stomach, the data from Bevan *et al.* (1994) were reanalysed. An equation was derived that would estimate EE from f_H on a mass specific basis that was independent of the mass of the animal at capture. The derived equation was:

$$\dot{V}_{O_2} = 0.00466f_H^{1.61}, r^2 = 0.79 \quad (2)$$

where \dot{V}_{O_2} is in ml min⁻¹ kg⁻¹. Measurements were converted to W kg⁻¹ by assuming that 1 ml O₂ has an energy equivalent of 20.112 J. Mean values are displayed as \pm s.e. Probability levels are deemed significant at the 95% level. Where statistical tests are used, the test name is given along with the probability.

3. RESULTS

(a) General information on birds and data

Heart rate data loggers (HRDL) were recovered from 24 black-browed albatrosses; 10 from 1991–92 and 13 from 1992–93. The unrecovered bird in 1991–2 was recaptured the next season when the HRDL, but unfortunately not the data it had contained, was recovered. Data on f_H and T_{ab} were successfully recorded from 18 black-browed albatrosses over a total of 412 days (mean number of days per bird = 22.9 ± 1.3 days). Table 1 provides data on the birds used, the timing of deployment, and the other instruments used. There was no difference over the monitoring period between the breeding success of implanted birds and non-implanted birds, however, the growth rates of the chicks were not recorded. However, in the 1991–2 field season, 55.6% of the implanted birds successfully hatched chicks and raised them to at least mid chick-rearing phase. This compares with 46.1% success to this stage in control colonies (P. A. Prince, unpublished data).

The times of departure from and arrival in the colony of an implanted animal could be estimated from the f_H traces (see figure 1) and checked by observing the birds in the colony. The mean foraging trip duration was 9.0 ± 1.2 days (range = 5.6 to 12.8 days) during incubation, and 2.5 ± 0.2 days (range 0.75–5.25 days) during the brooding period. During chick rearing, the birds visited the nest for only short periods of time. It was, therefore, only possible to monitor the duration of a visit of the birds with radio transmitters (i.e. the birds with satellite transmitters) using recording receivers that allowed the automated detection of

Table 1. *Basic information about the black-browed albatrosses used in the field*

(Mass is the mass of the birds at the start and end of the monitoring period. Date is the date that the data loggers were implanted and removed. Duration is that of the recording period. SWS and PTT are marked with a '+' if the bird was equipped with a salt water switch or a satellite transmitter, respectively.)

bird	mass		date		duration		SWS	PTT	notes
	start	end	start	end	days				
1_91	3.6	3.0	25/11/91	18/12/91	23	—	—		
2_91	3.9	4.1	25/11/91	18/12/91	23	—	—		
3_91	4.0	4.6	26/11/91	26/12/91	30	—	—		
4_91	3.0	3.2	26/11/91	26/12/91	30	—	—		
6_91	3.1	3.2	30/12/91	26/01/92	27	—	—	deserted	
7_91	4.9	3.9	30/12/91	19/1/92	20	—	—		
10_91	4.1	4.2	31/12/91	20/1/92	20	—	—		
12_91	3.7	3.5	31/12/91	20/1/92	20	—	—		
1_92	3.5	3.9	17/12/92	30/12/92	13	—	—	deserted	
3_92	3.8	4.2	17/12/92	13/1/93	27	—	—		
6_92	3.8	3.1	02/1/93	21/01/93	19	—	—		
7_92	3.9	3.5	07/1/93	05/02/93	29	+	—		
8_92	3.1	3.1	08/1/93	02/2/93	25	+	—		
9_92	3.4	3.8	08/1/93	11/02/93	30	+	—	implanted 33 days	
10_92	3.1	3.7	08/1/93	05/02/93	28	+	—		
11_92	3.4	3.7	08/1/93	10/02/93	30	+	—	implanted 32 days	
12_92	3.1	3.1	19/2/93	11/03/93	20	—	+		
13_92	3.3	3.4	19/2/93	19/03/93	28	—	+		

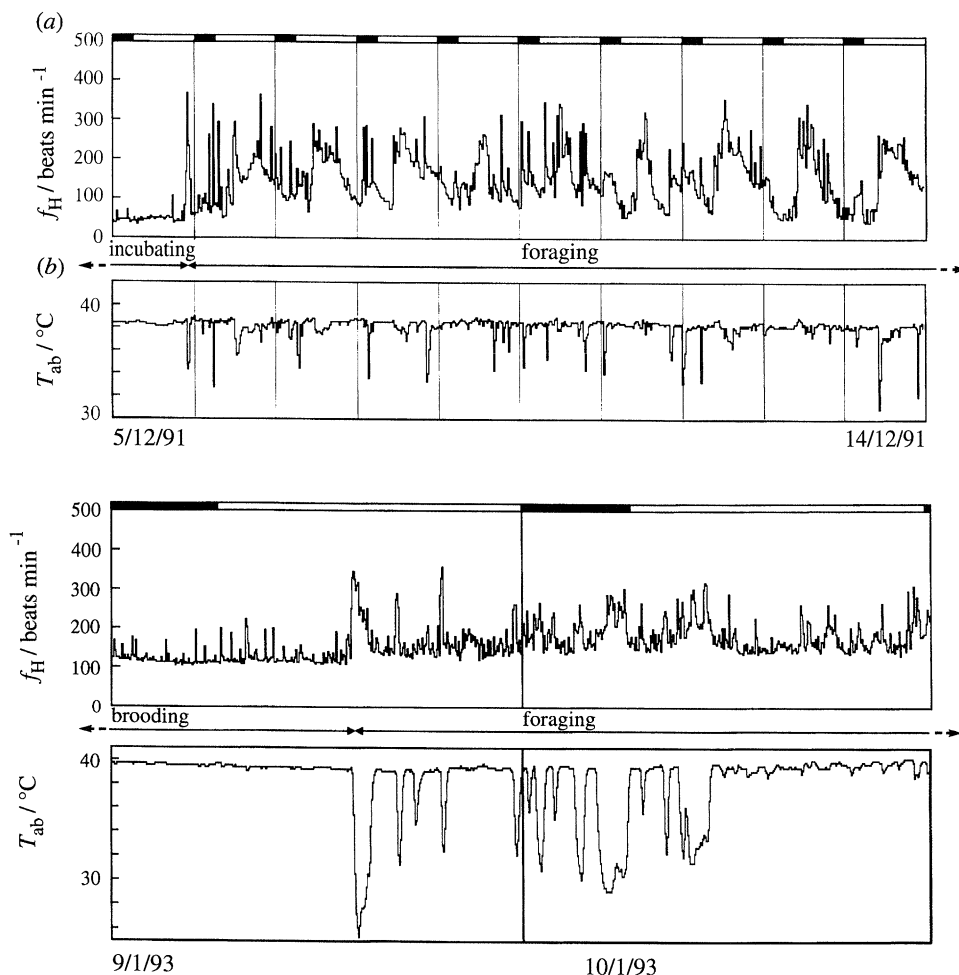


Figure 1. Traces of heart rate (f_H) (beats min^{-1} ; top trace) and abdominal temperature (T_{ab}) ($^{\circ}\text{C}$; bottom trace) obtained from two free-ranging black-browed albatrosses. Heart rate was sampled at 30 s intervals and temperature every 60 s. The dark bars above the heart rate trace indicate periods of darkness. (a) Ten days of data obtained during incubation. (b) Two days of data obtained during brooding.

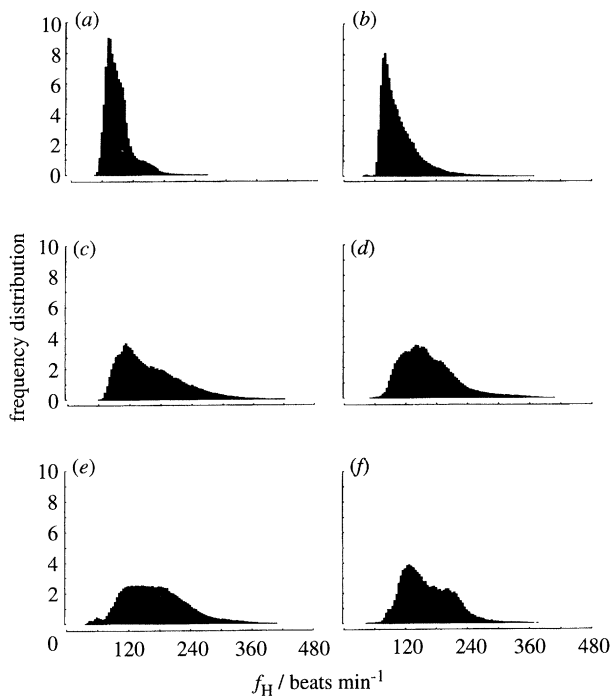


Figure 2. Frequency distributions of heart rate (f_H) (beats min^{-1}) during different activities and phases of the reproductive cycle of the black-browed albatrosses. The distributions are the means from all the birds performing that behaviour. Heart rate frequencies are counted over 4 beats min^{-1} intervals, and presented as a percentage of the total number of data values recorded for that behaviour. (a) on nest, incubation; (b) on nest, brooding; (c) foraging, incubation; (d) foraging, brooding; (e) foraging, chick rearing; (f) deserted.

their presence. In these birds the average time spent in the colony was 10.8 ± 1.0 min which is very similar to values of 13.2 ± 5.9 min, ($n = 534$) for visits by birds with only radio-transmitters in 1992/3 (P. A. Prince, unpublished observations).

(b) Heart rate data

(i) General

Figure 1 shows typical traces of f_H and T_{ab} from free-ranging black-browed albatrosses. During incubation and brooding, when the birds are at the nest, f_H and T_{ab} are relatively stable, but when at sea and foraging there are large changes in both variables.

(ii) Changes with reproductive phase

The frequency distribution of f_H when at the nest (during the incubation and brooding shifts) is extremely positively skewed with a mode of 80 beats min^{-1} and a median of 82 beats min^{-1} (see figures 2a, b). The maximum recorded f_H when at the nest was 420 beats min^{-1} during incubation and 408 beats min^{-1} when brooding, but 95% of all f_H were below 152 beats min^{-1} and 184 beats min^{-1} during these respective activities. Heart rates were more normally distributed when the birds were foraging at sea during the brooding and chick rearing phases (see figures 2d, e), but remained slightly negatively skewed while at sea during the incubation period (see figure 2c). The

f_H data obtained from the birds that had deserted were also slightly skewed (see figure 2f). Modal f_H when foraging during the incubating, brooding and chick-rearing phases and when they had deserted were 116 beats min^{-1} , 140 beats min^{-1} , 148 beats min^{-1} and 128 beats min^{-1} respectively, whereas maximum f_H were 448 beats min^{-1} , 420 beats min^{-1} , 416 beats min^{-1} and 376 beats min^{-1} . Nevertheless, of all the f_H recorded during foraging, regardless of reproductive phase, 95% were below 284 beats min^{-1} (see figures 2c–f).

(iii) Diel variation

When the f_H data were partitioned according to the time of the day that they were recorded, the frequency distribution of the f_H from incubating birds showed very little variation with time. During brooding, however, there was a distinct variation with time (see figure 3). Between 09h00 and 15h00, f_H was fairly stable, whereas at other times it was distinctly bimodal with modes at 80 beats min^{-1} and 130 beats min^{-1} . When at sea during the incubation period, f_H distribution was skewed to the lower f_H at around midday but was more normally distributed around midnight (see figure 3). This pattern was also seen, but to a lesser extent, in birds that were foraging during the brooding and chick-rearing periods (see figures 3). The pattern of frequency distributions of the birds that had deserted the nest were similar to those obtained in the foraging birds during incubation (see figure 3).

The frequency distributions suggest that there are strong diel variations in f_H (and hence activity). Figures 4a–c represent data obtained from individual foraging birds during the incubation phase and show clear peaks in mean f_H at specific times of the day (see figures 4a–c). However, this is less obvious or absent in other birds (see figures 4d–i). Even so, it should be noted that the peak values of mean f_H of the foraging birds during incubation occur at different times of the day for different individuals (see figures 4a–c).

When the data from all the birds are averaged, there was very little variation in f_H with time. Incubating or brooding birds had a mean f_H of approximately 110 beats min^{-1} regardless of the time of day. Likewise, birds during the brooding and chick-rearing periods and the birds that had had a mean f_H of approximately 160 beats min^{-1} , which varied little with time. It is only in the birds foraging during the incubation phase that any periodicity was exhibited, with peak f_H of 205 beats min^{-1} occurring at 01h00 (GMT).

(c) Energy expenditure

(i) Metabolic rate over the phases of the reproductive cycle

The main purpose of this study was to use the f_H data described above to estimate the EE of the free-ranging birds. Figure 5 shows the estimated daily of five individuals during different phases of the reproductive cycle. The estimated EE of individual birds varied considerably during the monitoring period according to their behaviour. The estimated EE of the birds when on the nest during incubation and brooding were 2.22 ± 0.12 and 2.42 ± 0.17 W kg^{-1} respectively

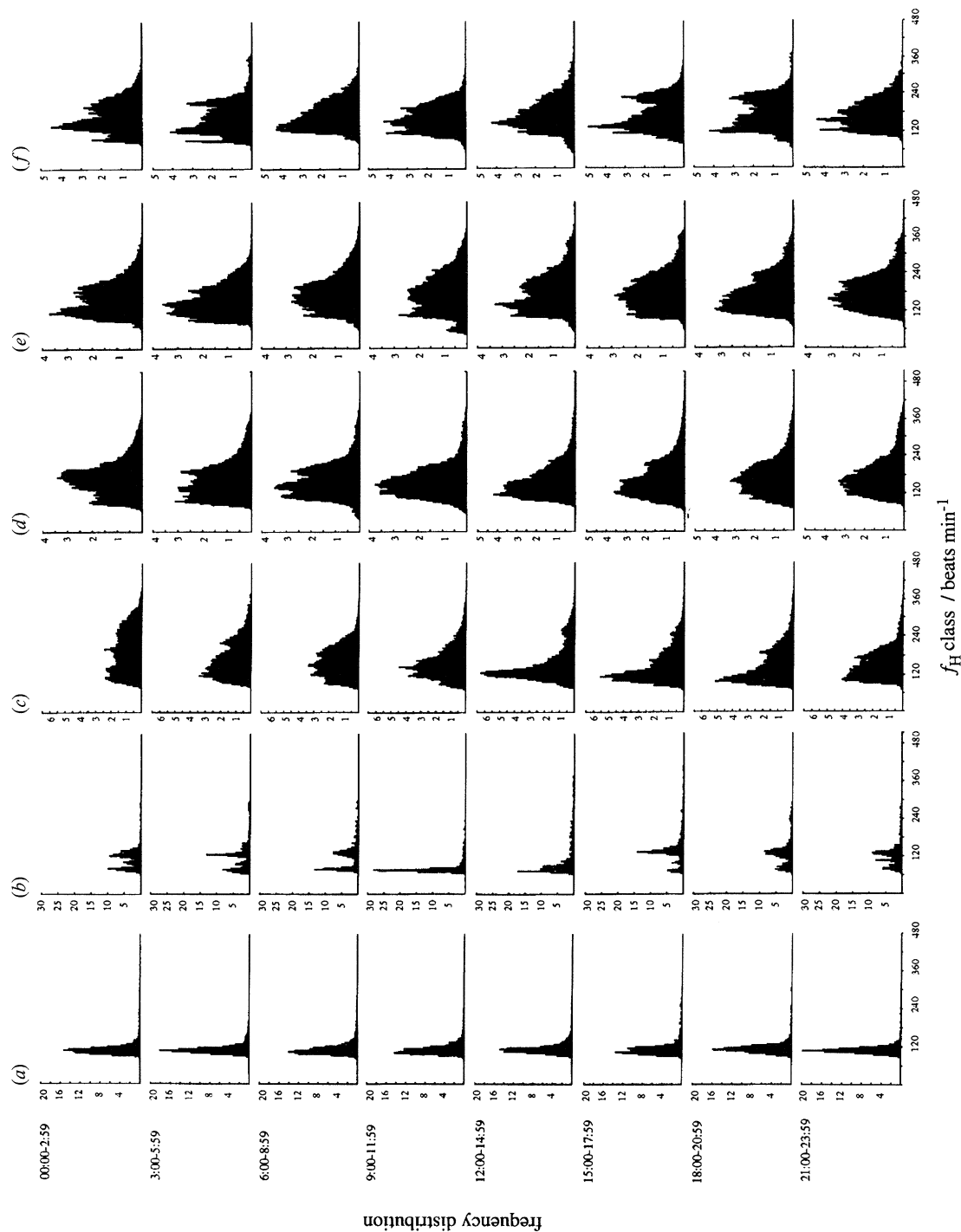


Figure 3. Frequency distribution of heart rate (f_H) (beats min^{-1}) for black-browed albatrosses during different activities and phases of the reproductive cycle at different times of the day. See figure 2 for further details. (a) on nest, incubation; (b) on nest, brooding; (c) foraging, incubation; (d) foraging, brooding; (e) chick rearing; (f) deserted.

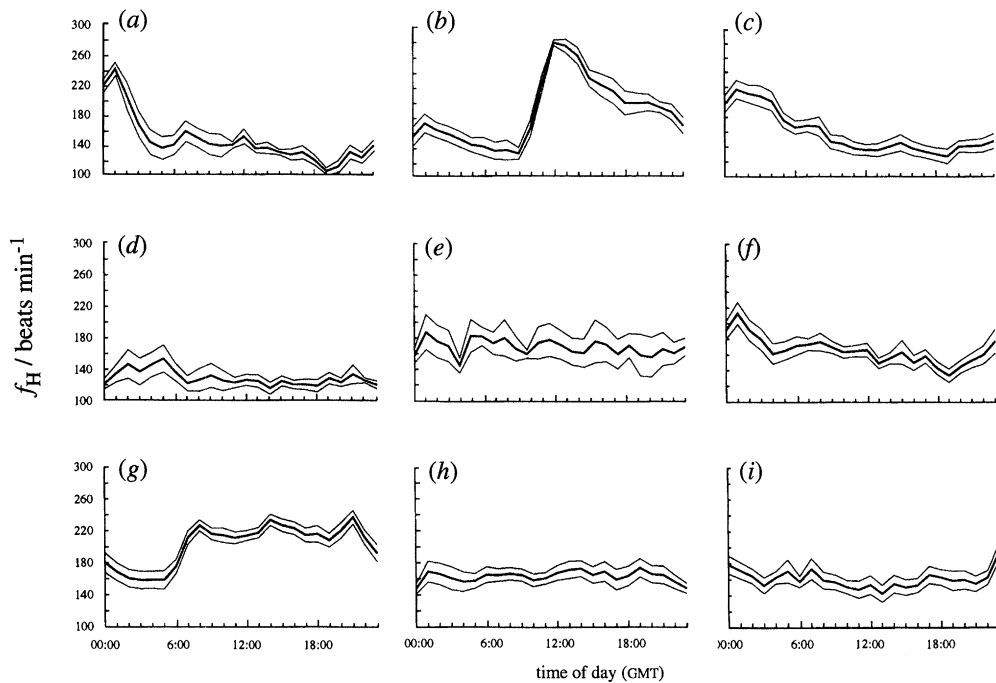


Figure 4. Mean heart rates (f_H) (beats min^{-1}) of 9 individual black-browed albatrosses ($a-i$) during foraging, related to different times of the day. The solid lines are the hourly means and the dashed lines \pm s.e. The means were averaged over all days that the bird was foraging during one phase of the reproductive cycle. Birds a , b and c were foraging during incubation, d and e during brooding, f and g during chick-rearing, and birds h and i had deserted the nest.

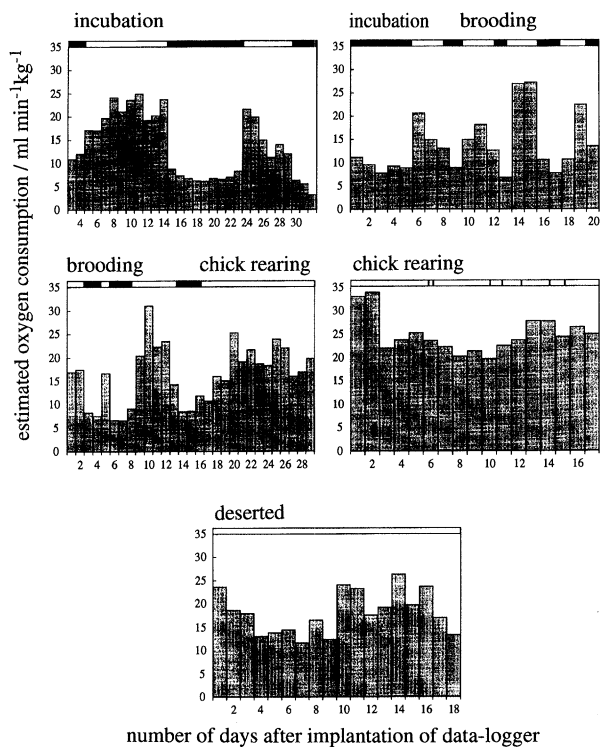


Figure 5. The variation of mean oxygen consumption ($\text{ml min}^{-1} \text{kg}^{-1}$), estimated from heart rate averaged over each day, of individual black-browed albatrosses as a function of time. The bars above each graph represent time spent at the nest (black = incubating, grey = brooding, lines = chick feeding)

which increased when the birds were foraging during incubation, brooding and chick-rearing to 4.72 ± 0.39 , 4.63 ± 0.39 and $5.80 \pm 0.58 \text{ W kg}^{-1}$ respectively, where-

as the deserted birds had an estimated EE of $5.44 \pm 0.40 \text{ W kg}^{-1}$ (see figure 6). A one-way ANOVA showed that there were significant differences between these rates ($N = 43$, $p < 0.001$). A Bonferroni *post hoc* test showed that there was no significant difference between the EE of brooding and incubating birds and that there was no significant difference between the EE of birds foraging over the different reproductive phases. There was, however, a significant difference between the 'on nest' and 'foraging' EE.

The mean EE over the entire incubating/foraging and brooding/foraging cycles were $3.63 \pm 0.25 \text{ W kg}^{-1}$ and $3.54 \pm 0.19 \text{ W kg}^{-1}$ respectively, and are significantly lower than that during the chick rearing phase (ANOVA, $N = 43$, $p < 0.001$) when a high EE ($5.80 \pm 0.58 \text{ W kg}^{-1}$) is maintained almost continuously.

(ii) Metabolic cost of specific behaviours

The data recorded by the sws gave information on whether the birds were on the water or flying while the satellite transmitter gave information on the distance that the birds travelled. By combining these data with the simultaneous measurements of f_H it was possible to estimate the metabolic costs of various activities.

Figure 7 depicts a trace from a black-browed albatross with a sws attached. There was no apparent pattern to the time spent on the water with nearly equal time spent on the sea during both the day and night. While at sea, the birds spent a significantly greater proportion of their time flying than on the water, $30.5 \pm 4.4\%$ on the water and $69.1 \pm 4.5\%$ in flight (paired *t*-test, $N = 5$, $p = 0.013$). It was impossible to estimate the energy expended performing any

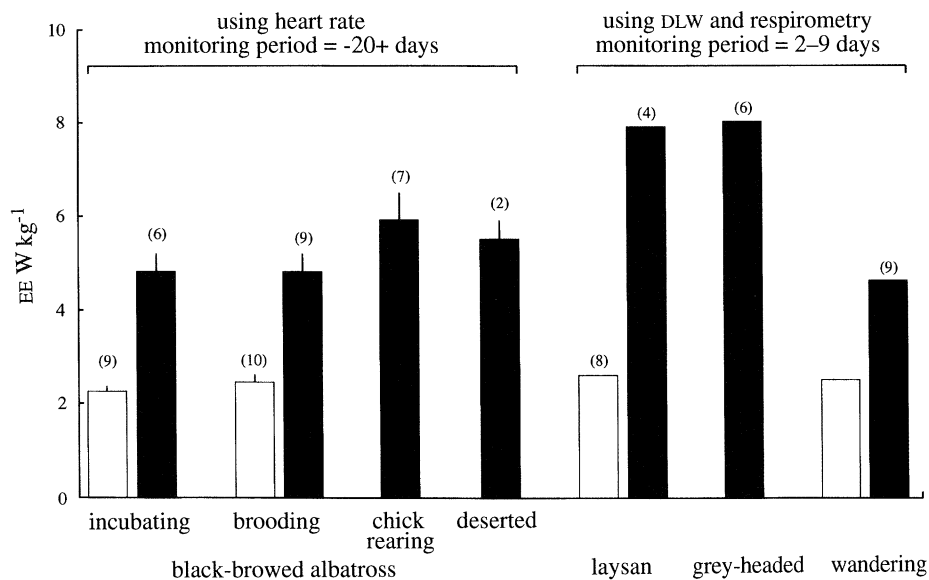


Figure 6. Mean energy expenditure (EE) ($W\ kg^{-1}$) of different species of albatross. Light columns are from birds at the nest, solid bars when birds were foraging. The vertical lines and numbers above each column represent the s.e. of each mean value and the number of birds used in each study. Data for: black-browed albatross, estimated from heart rate (this study) ($3.58\ kg$); Laysan albatross from DLW (Pettit *et al.* 1988) ($3.07\ kg$); grey-headed albatross from DLW (Costa & Prince 1987) ($3.53\ kg$); incubating wandering albatross from respirometry (Brown & Adams (1984); foraging wandering albatross from DLW (Adams *et al.* 1986) ($8.41\ kg$).

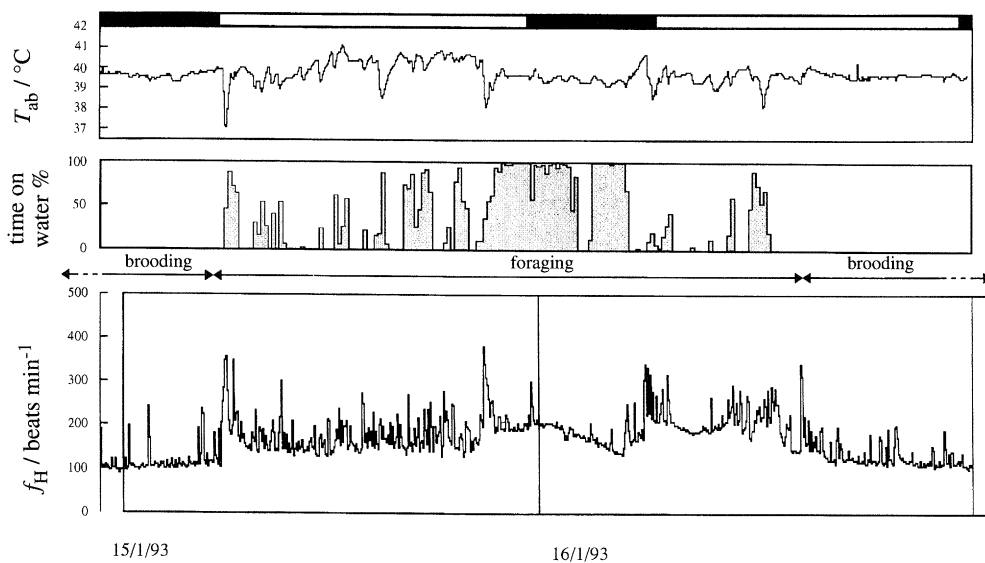


Figure 7. Traces of abdominal temperature (T_{ab}) ($^{\circ}C$, top trace), activity (% time spent on the water, middle trace) and heart rate (f_H) (beats min^{-1} , bottom trace) of a black-browed albatross during the brooding phase. See figure 1 for further details.

of these activities (flight or on the water) unless that behaviour lasted for an entire 12 min recording period due to the time resolution of the sws. Analysis was therefore restricted to those 12 min periods during which the recorder was wet or dry for the whole time. The mean MR of the birds when on the water was $5.77 \pm 0.41\ W\ kg^{-1}$ which was not significantly different from the rate when the birds were flying ($6.21 \pm 0.24\ W\ kg^{-1}$, $n = 5$, paired t -test $p = 0.450$).

The distance travelled, the ground speed and the EE between each location is provided by the satellite transmitter equipped birds. Even though several hours can pass between successive uplinks and hence the

estimates of speed may be very imprecise, a high mean ground speed between two points implies constant flight and conversely a very low mean ground speed will imply that the bird is spending very little time in flight. Although some high EE s appeared to coincide with high ground speeds only a very weak correlation existed. Furthermore, even when the data were averaged over different ground speed classes, thereby eliminating some of the inherent variation, the EE was still independent of ground speed (see figure 8).

From the data obtained from the PTT and the radiotransmitter, it was possible to estimate the energy expended by the birds over the first (outward) and the

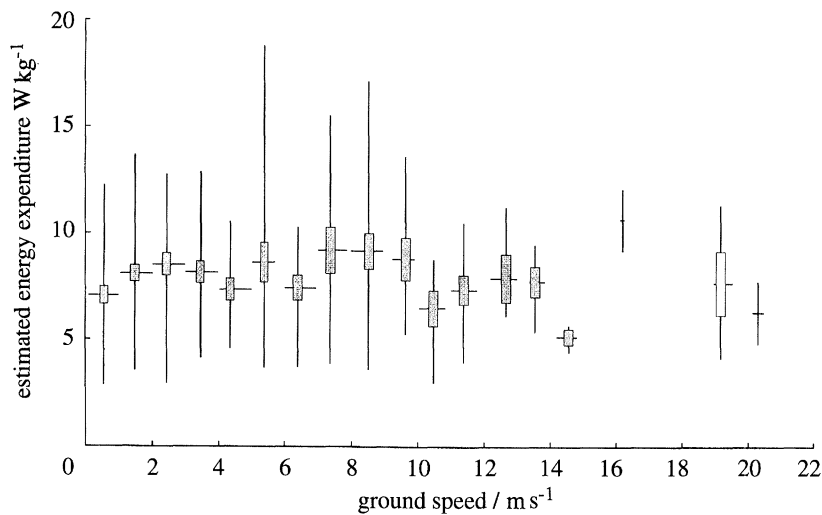


Figure 8. Estimated energy expenditure (W kg^{-1}) as a function of mean ground speed (m s^{-1}) of two satellite tracked black-browed albatrosses. Vertical and horizontal lines are the ranges of the energy expenditures and ground speeds respectively. The box represents \pm s.e. about the mean of the estimated energy expenditure.

Table 2. Energetic costs of flying to and from the colony of two implanted black-browed albatrosses equipped with satellite transmitters

(Duration: time between leaving colony and first position from satellite transmitter. Distance: distance between colony and first position. Speed: mean ground speed to first position. Energy expended: energy expended while travelling.)

	duration	distance	speed	energy expended	
	min	km	m s^{-1}	W kg^{-1}	N
leaving colony	116 ± 18	52.1 ± 11.3	8.5 ± 1.7	7.15 ± 0.70	10
returning to colony	103 ± 11	51.2 ± 10.2	8.3 ± 1.2	9.74 ± 0.41	12
	n.s.	n.s.	n.s.	$p = 0.0335$	

last (return) leg of a foraging trip (see table 2). There was no significant difference between the duration, distance or mean ground speed of the outward and return journeys. However, the energy expended by the birds leaving the colony was significantly lower than that when they returned (t -test, $N = 22$, $p = 0.0335$).

(d) Abdominal temperature

When on the nest, the mean T_{ab} was 39.3 ± 0.4 °C and changed very little with time (see figure 1). However, when at sea, T_{ab} showed large variations, presumably relating to the behaviour of the bird, with large variations (> 0.5 °C between successive readings) often occurring. All of these large drops in T_{ab} occurred when data from the sws indicated that the bird had spent time on the water. None were seen when the device was completely dry. The mean temperature to which the abdominal cavity dropped was 34.2 ± 1.0 °C with a maximum temperature drop of 6.9 ± 1.8 °C, to a mean minimum value 32.5 ± 2.0 °C. In addition, all birds showed a drop in T_{ab} , to an average of 36.5 ± 0.5 °C, soon after leaving the colony.

4. DISCUSSION

(a) Effect of implantation

There is obviously an effect, even if only in the short term, on the animal caused by the operative procedures used to implant the HRDL and this has to be considered

when assessing the data obtained by this technique. The f_{H} of the birds when on the nest were elevated after implantation of the HRDL, but after two days the resting rates were not significantly different from those at the end of the recording period (on average 22 days later). This contrasts with the study by Stohr (1988) which showed that mean f_{H} in implanted animals took up to 2 weeks to decline to baseline values. This difference between studies may be attributable to the small size of the animals used by Stohr (1988). Behavioural considerations also indicate that the implantation did not adversely affect the birds in the present study. The durations of the foraging trips undertaken by the implanted birds did not differ significantly from those of the non-implanted birds in the colony, and were within the range reported by Tickell & Pinder (1975). In addition, the breeding success of the implanted birds was no different from that of other birds. It is therefore apparent that, although the operation does have a minor physiological effect over the first two days, subsequently the birds appear to be behaving normally.

(b) Energy expenditure

(i) Frequency distribution of heart rate

One factor that is important when using f_{H} to estimate \dot{V}_{O_2} is that the calibration procedure covers the range of f_{H} found in the wild birds (Nolet *et al.* 1992; Bevan *et al.* 1994). For the black-browed albatross, f_{H}

was calibrated against birds walking on a treadmill (Bevan *et al.* 1994). From these birds, the range of f_H over which was measured were between 66 beats min^{-1} and 409 beats min^{-1} . The frequency distributions (see figure 2) show that only 0.3% of the f_H of free-ranging birds fall outside of this range. Jungius & Hirsch (1979) measured f_H in incubating waved albatrosses (*Diomedea irrorata*) on the Galapagos Islands using a microphone placed in the nest to monitor the sound of the heart beating. They recorded f_H of approximately 65 beats min^{-1} which are 40% lower than the f_H of incubating black-browed albatrosses. This difference may be due to the waved albatross, a tropical species, having a lower thermoregulatory requirement.

Another aspect to be revealed by the frequency distributions is that incubating and brooding birds were, not surprisingly, relatively inactive while at the nest. There were however more high f_H in the brooding than in the incubating birds and probably represent the activity imposed on the bird by the chick for example, through having to stand up to feed the chick. It may also reflect the higher activity in the colony, and hence disturbance, during this period as the birds are exchanging with their partners more frequently.

(ii) Daily variation

The estimates of EE derived from f_H can be compared with those obtained for albatrosses by other studies using DLW and respirometry (see figure 6). The energy expended by incubating birds is approximately the same across all species studied so far, viz black-browed, wandering (Brown & Adams 1984) and Laysan (Pettit *et al.* 1988) albatrosses. However, the estimates of EE of foraging birds derived from f_H are lower than those from DLW (Adams *et al.* 1986; Costa & Prince 1987; Pettit *et al.* 1988). This difference could be due to the wide range of EES exhibited by individual birds during foraging trips (see figure 5). It could also be due to an overestimate of EE from the DLW technique, as the birds lose body mass during incubation and brooding which is replaced during the foraging period. This may cause the isotopes to be incorporated into the tissues which could introduce an error into the estimate from DLW (Nagy & Costa 1980; Tatner & Bryant 1989). This anabolism may also introduce another error, as the RQ that is used to estimate energy consumption from the rate of CO_2 production will be incorrect. In addition, the birds may have been stressed by the handling procedures required by the DLW method. The recovery from the implantation procedure can last up to 2 days and we have ignored this section of the data. Although the recovery from the handling in the DLW procedure is unlikely to last this long, it may be a factor in raising measured EE, especially over the initial part of the relatively short experimental periods involved.

There is an increase in the overall energy expended at different phases of the reproductive cycle, from incubation through brooding to chick rearing. If the birds are spending ~50% of their time at the nest during the incubation and brooding periods then the overall cost over an incubating(brooding)/foraging cycle will be lower than when the bird spends most of its time foraging i.e. during the chick-rearing period.

Thus the energy used by a breeding pair during incubation will be the sum of the energy expended by the incubating bird plus that expended by the foraging partner. A similar situation would apply to birds during the brooding phase. During the chick rearing phase, however, both partners will be foraging. The overall costs to a pair would, therefore, be 6.9 W kg^{-1} during incubation, 7.1 W kg^{-1} during brooding and 11.6 W kg^{-1} during the chick-rearing phase.

It is interesting to note that the birds that deserted, and were therefore only having to maintain themselves, had an estimated EE that was not significantly different from the foraging rates of breeding birds, but was statistically higher than the overall EE of the birds during incubation or brooding. This implies that the energy cost of a dependent chick during early brooding is relatively small. Alternatively, the birds that deserted may have diverted resources into other activities or physiological processes, for example, courtship or moult. The former is a possibility as they were seen displaying with other birds when they returned to the colony.

(iii) Hourly variation

The birds spent approximately 9 days at sea before returning to the nest site during the incubation phase but during the brooding period, foraging trips lasted, on average, only 2.5 days (cf. Tickell & Pinder 1975). Each foraging trip is comprised of the time spent travelling to and from the foraging area plus the time spent at that site. If the birds are foraging in the same areas, irrespective of reproductive phase, then the time taken to get to and from these areas will, presumably, be the same. Consequently, the birds during the brooding phase will have a proportionally shorter time for foraging. Any circadian rhythms in EE (low EE during the day, high EE during the night as in the incubation phase) will therefore be masked by the inclusion of the energy expended during the travel periods. One possible explanation for the rhythmicity in f_H displayed by the foraging birds during incubation is that the birds can concentrate their activity at the optimal foraging time i.e. during the night when the squid and krill come to the surface and are, therefore, easier to catch (Croxall & Prince 1994). The brooding and chick-rearing birds will have to be more opportunistic in their foraging activity as they are compromised by the need to return to the nest to feed the chick. Certainly, the birds that were equipped with sws during the brooding phase showed no obvious pattern to the time spent on the water which indicates that they were not selecting a particular time to forage but were indeed foraging opportunistically.

(iv) Energetics of flight

One of the advantages of using f_H is that a much more detailed analysis of the energetics can be obtained. A gross analysis of the data from the satellite tracked birds masks some interesting underlying features of the data. If the flight track of a single foraging trip is plotted along with the computed variables between two locations and the f_H and T_{ab}

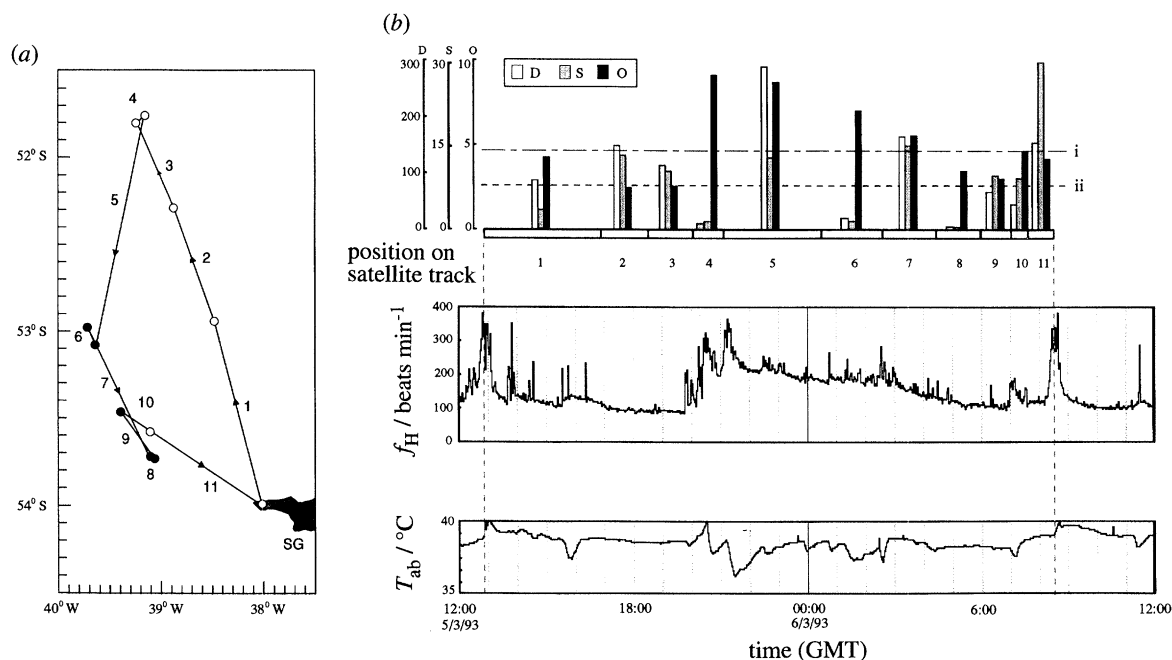


Figure 9 (a) Flight track of a single foraging trip from S. Georgia (SG) by a black-browed albatross equipped with a satellite transmitter and data logger. Circles represent the position at each satellite uplink, with solid circles showing positions during the hours of darkness. The arrows show the path travelled between each successive position, each path being numbered consecutively. (b) Top graph. Distance travelled (D, km), ground speed (S, m s⁻¹) and estimated energy expenditure (O, W kg⁻¹). Data are computed for each leg of the flight track depicted in (a). The horizontal bars represent the time between each satellite position (shading is for clarity only). Mean ground speed (horizontal broken line (i) is from Alerstam *et al.* (1993). The incubating metabolic rate (horizontal broken line ii) is that measured while on the nest during incubation from the present study (W kg⁻¹). Middle and bottom graphs. Heart rate and abdominal temperature traces over the same period. The vertical dashed lines joining the three graphs show when the bird leaves and returns to the colony.

data (see figure 9) an interesting picture emerges. On leg 2 of the flight track, the bird travelled 80.1 km in 1.7 h, a mean ground speed of 13.1 m s⁻¹. This is very similar to the mean speed of 12.9 m s⁻¹ that Alerstam *et al.* (1993) report for visually tracked black-browed albatrosses, and suggests that the bird was flying continuously over leg 2 of the flight track. This supposition is supported by the T_{ab} data which show very little variation, again indicating that the bird was not on the water. Furthermore, the EE is very low over this period (2.4 W kg⁻¹), barely greater than the EE during incubation (2.2 W kg⁻¹), and much lower than the predicted BMR of the black-browed albatross (3.1 W kg⁻¹) (Ellis 1984). The reverse is true for leg 4.

Over this portion of the flight track, the overall distance travelled is very short, only 6.3 km, with a mean ground speed of 1.6 m s⁻¹, indicating that the bird is relatively stationary and on the water for most of the time or is actively flying within a restricted area. Over this period the bird exhibits the highest rate of EE at 8.8 W kg⁻¹, which suggests that the bird is engaged in some form of activity, probably feeding. Further evidence for this comes from the large changes in T_{ab} that occur during this period indicating ingestion events (see figure 9).

The birds in the present study spent 31% of their time while at sea on the water; 69% of the time at sea is therefore spent in flight. The overall energy cost of flight, as estimated from the f_H data, was 6.2 W kg⁻¹. This is much lower than the estimate of 9.8 W kg⁻¹ derived by Costa & Prince (1987) and is only two times

the estimated BMR (Ellis 1984) but is comparable to the 2 × BMR measured in gliding gulls (Baudinette & Schmidt-Nielsen 1974). However, as has been illustrated by the satellite data, the cost of flight may be considerably lower than this.

A possible explanation is that, when searching for prey patches, the birds travel with the minimum expenditure of energy, flying at 120–50° to the prevailing wind (Alerstam *et al.* 1993) and do not actively set a course i.e. they are being carried by the wind. Having located their prey, however, they may then have to deviate from the direction dictated by the wind in order to exploit the food source. This may also apply when the bird decides to return to the nest, when the wind may not be in the optimum direction. The bird would then have to set its own course which would probably involve a more active use of the wind and waves which in turn would lead to an increase in work performed by the wing muscles. This may explain why the birds have a higher rate of EE when making the return journey when compared with the outward one.

Other studies have tried to estimate the cost of flight in albatrosses by making the assumption that, when on the water, the EE of the birds is equivalent to the BMR (Adams *et al.* 1986; Costa & Prince 1987). From the present study, this is obviously not the case, and there are a number of factors which would argue against this assumption. Firstly, the birds will be floating on water which will be at a temperature of approximately 2–3 °C which would, in itself, cause a substantial increase in EE (Jenssen *et al.* 1989; Bevan & Butler

1992; Bevan *et al.* 1994). Secondly, part of the time that the albatrosses are on the water will be spent feeding. Such activity, particularly when it occurs in flocks, and regardless of whether it is associated with prey aggregations (Harrison *et al.* 1991) or with fishing vessels (Ashford *et al.* 1994), is likely to be energetically expensive. This is especially relevant if the birds are having to dive as well (Prince *et al.* 1994).

From the sws data, the overall EE of the birds when on the water is not significantly different from the cost of flight at approximately 2 times the BMR. If the data of Costa & Prince (1987) and Adams *et al.* (1986) are re-analysed with this in mind, then the cost of flight from these studies would be 7.5 W kg^{-1} and 4.6 W kg^{-1} , or 2.5 and 1.8 times the estimated BMR respectively. These rates are comparable with those found in the present study and are further evidence that the energy cost of the different behaviours has to be determined and not merely assumed.

(c) *Abdominal temperature*

The large changes in T_{ab} recorded in the free-ranging birds (all of which occurred when the birds were on the water) have a number of possible explanations. Wilson *et al.* (1992) found similar changes (both qualitative and quantitative) in temperatures of free-ranging wandering albatrosses equipped with stomach temperature probes. These temperature drops were attributed to feeding events as they were very similar to the results obtained from captive penguins equipped with temperature probes that were fed known volumes of cold water. Wilson *et al.* (1992) concluded that, for the albatrosses, water ingestion was unlikely and that all large temperature drops are due to feeding events. However, in all our brooding and incubating birds, a large drop in T_{ab} was seen within a few minutes of the birds leaving the colony (see figures 1 and 7). This would be too short a time for the birds to have reached the foraging grounds and is consistent with observations that albatrosses leaving the colony form rafts on the water nearby where they preen extensively and probably ingest some water. The drop in T_{ab} would also be accentuated by the lack of food in the stomach of the bird as there would be no mixing. Nevertheless, it is most likely that the other large drops in T_{ab} are due primarily to the ingestion of prey items.

Comparison of the T_{ab} and activity recorder data suggests that landing on the water can also produce a change in T_{ab} , presumably because of conductance to the HRDL via the brood patch. With more data from birds with a sws attached, it may well be possible to differentiate between ingestion of water, ingestion of prey and landing on the water. However, small drops in T_{ab} are much more difficult to interpret and further discussion of this fascinating topic lies outside the scope of the present paper.

This is the first study to have used extensively f_{H} to determine the energy consumption of a free-ranging sea-bird. The advantages of using this technique are that data can be obtained over much longer time periods while still retaining a high time resolution. As a consequence of this, it is now possible to assign

energetic costs directly to different behaviours while the bird is at sea, for example, flight or foraging which, as has been shown by this study, is very important when estimating the overall energy costs of a species. At the same time it should be noted that behavioural information, which at present can be obtained only via externally mounted instruments, forms a necessary part of such a study in terms of the interpretation of the data. It can therefore be seen that, through the use of f_{H} , it is now possible to address biological and ecological questions that have hitherto been impossible.

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