

RESEARCH ARTICLE

Heart rate and estimated energy expenditure of flapping and gliding in black-browed albatrosses

Kentaro Q. Sakamoto^{1,*}, Akinori Takahashi^{2,3}, Takashi Iwata^{2,†}, Takashi Yamamoto³, Maki Yamamoto⁴ and Philip N. Trathan⁵

¹Graduate School of Veterinary Medicine, Hokkaido University, Sapporo 060-0818, Japan, ²Department of Polar Science, The Graduate University for Advanced Studies, Tachikawa, Tokyo 190-8518, Japan, ³National Institute of Polar Research, Tachikawa, Tokyo 190-8518, Japan, ⁴Department of Bioengineering, Nagaoka University of Technology, Nagaoka 940-2188, Japan and ⁵British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

*Author for correspondence (sakamoto@vetmed.hokudai.ac.jp)

†Present address: International Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo, Chiba 277-8564, Japan

SUMMARY

Albatrosses are known to expend only a small amount of energy during flight. The low energy cost of albatross flight has been attributed to energy-efficient gliding (soaring) with sporadic flapping, although little is known about how much time and energy albatrosses expend in flapping *versus* gliding during cruising flight. Here, we examined the heart rates (used as an instantaneous index of energy expenditure) and flapping activities of free-ranging black-browed albatrosses (*Thalassarche melanophrys*) to estimate the energy cost of flapping as well as time spent in flapping activities. The heart rate of albatrosses during flight (144 beats min⁻¹) was similar to that while sitting on the water (150 beats min⁻¹). In contrast, heart rate was much higher during takeoff and landing (ca. 200 beats min⁻¹). Heart rate during cruising flight was linearly correlated with the number of wing flaps per minute, suggesting an extra energy burden of flapping. Albatrosses spend only 4.6±1.4% of their time flapping during cruising flight, which was significantly lower than during and shortly after takeoff (9.8±3.5%). Flapping activity, which amounted to just 4.6% of the time in flight, accounted for 13.3% of the total energy expenditure during cruising flight. These results support the idea that albatrosses achieve energy-efficient flight by reducing the time spent in flapping activity, which is associated with high energy expenditure.

Key words: black-browed albatross, *Thalassarche melanophrys*, flight, flapping, gliding, heart rate, energy expenditure, accelerometer.

Received 6 September 2012; Accepted 28 April 2013

INTRODUCTION

Flapping activity is considered to be one of the major contributors to energy expenditure during flight. Hence, many birds try to save energy by reducing the amount of flapping (Videler, 2005; Tobalske, 2007). Birds employ diverse flight styles, including intermittent flight, formation flight and soaring (Rayner, 1977; Pennycuik, 2002; Weimerskirch et al., 2001). Albatrosses provide a notable example of how birds reduce energy expenditure during flight, as they have the lowest energy cost of transport by unit mass and distance of all bird species examined to date (Videler, 2005). Albatrosses have several features that allow such low-cost flight. The high aspect ratio of their wings enables prolonged gliding until they lose altitude (Pennycuik, 1982). Moreover, these birds use a soaring technique that extracts power for flight from ambient wind over waves during gliding (Pennycuik, 2002; Richardson, 2011).

To better understand the efficiency of their low-cost flight, assessing how much energy and time seabirds expend flapping and gliding during flight is essential, but few studies have examined this issue. A previous study yielded somewhat surprising results, as Cape gannet, *Morus capensis*, showed an increase in heart rate of only 20% during flapping flight compared with gliding (Ropert-Coudert et al., 2006). More data on energy cost of flapping for prolonged gliders such as albatrosses would provide new insight

into their unique style of flight. In addition, with the exception of observations from land and boats (Pennycuik, 1982), there have been few reports regarding the time spent flapping by albatrosses in the open ocean (Sato et al., 2009). Thus, to understand flight costs under natural conditions, it is necessary to monitor energy expenditure and flapping activity simultaneously.

The energy expenditure of pelagic seabirds during flight has been estimated using doubly labelled water and heart rate recording techniques. The doubly labelled water technique measures the energy expenditure through the turnover of stable oxygen and hydrogen isotopes in the blood, which reflect metabolic rate. The limitation of this technique is that it provides only a single energy expenditure value over the entire monitoring period. Several studies that applied the doubly labelled water technique simultaneously recorded whether the bird was in flight or on water and estimated the proportion of time spent in flight to determine the cost of flight (Birt-Friesen et al., 1989; Shaffer, 2011; Shaffer et al., 2001; Shaffer et al., 2004). Another technique, heart rate monitoring, measures the heart rate of the bird continuously during flight (Bevan et al., 1995; Butler et al., 1998; Pelletier et al., 2008). Heart rate can reflect the rate of oxygen consumption when both the stroke volume of the heart and the extraction of oxygen by the body tissues change in a systematic fashion (Fick, 1870). Although these values may

change and thus the relationship may not be linear, heart rate is correlated with the rate of oxygen consumption under most conditions (Butler et al., 2004; Green et al., 2009; Green, 2011). Thus, once the relationship between heart rate and the rate of oxygen consumption is established, properly calibrated and validated, heart rate can serve as a good indicator of energy expenditure. The advantage of this technique is the fine-scale, temporal resolution of the records.

Flapping involves rotation of the wing, which causes periodic motion of the body. Therefore, continuous measurement of body acceleration would allow the determination of flapping as a periodic signal. Measurements of acceleration are also applicable for monitoring the activity of free-ranging birds in remote areas (Yoda et al., 2001; Sato et al., 2008). The main difficulty of this approach is the complexity of the analysis when processing large amounts of data. However, Sakamoto et al. (Sakamoto et al., 2009a) developed algorithms to generate an ethogram from body acceleration records, which enables flapping signals to be extracted from acceleration records. Therefore, continuously recording heart rate and body acceleration with other behavioural parameters using animal-attached tags would be a promising approach to better understand the flight performance of birds under natural conditions.

In this study, we used electrocardiogram (ECG) recorders and accelerometers attached to free-ranging black-browed albatrosses [*Thalassarche melanophrys* (Temminck 1828)] to determine how heart rate varies in relation to flight mode and time spent flapping over the open ocean. Black-browed albatrosses have been studied extensively, including the relationship of heart rate to the rate of oxygen consumption and energy expenditure under natural conditions (Bevan et al., 1994; Bevan et al., 1995). The present study was performed to assess the energy cost of flight in relation to flapping and to compare the costs of different activities during a foraging trip. The characteristics of such a fine-scale time–energy budget should shed light on the flight performance of albatrosses.

MATERIALS AND METHODS

Fieldwork

Fieldwork was conducted at a black-browed albatross breeding colony on Bird Island (54°00'S, 38°03'W), South Georgia, in January 2005 and 2009, which corresponded to the chick-guarding period. This study was approved by the British Antarctic Survey and the University of Cambridge Animal Ethics Board prior to the commencement of fieldwork.

We equipped eight chick-rearing albatrosses at their nest sites; they were weighed and equipped with recorders (Table 1). The masses of the birds ranged from 3.05 to 4.25 kg. Three birds had both an ECG recorder and an accelerometer attached (see below), four birds had an accelerometer and an activity recorder attached and one bird had only an accelerometer attached. Animal handling times were always <30 min and all birds returned to the nest immediately after release before voluntarily departing on a foraging trip. Instrumented birds were recaptured after a single foraging trip lasting 3–4 days; all recorders were retrieved and data were downloaded. The timing of arrival at the nest could be easily identified from the acceleration data. Acceleration data recorded at the nest were omitted, and only the data during the actual foraging trip were used for analysis.

Instruments

The ECG recorder (UME-190-ECG; Little Leonardo, Tokyo, Japan) was 15 mm in diameter and 73 mm in length, with a mass of 24 g in air, and was used to measure heart rate (sampling frequency, 128 Hz). The recorder was composed of a data logger and three disposable electrodes connected to the logger with cables. Two of the electrodes were placed above and below the central part of the sternum to detect the electric potential difference, while the third electrode was placed on the back of the bird to act as a ground wire to reduce electrical noise (Yamamoto et al., 2009). All electrodes were made of gold-plated safety pins and were placed under the skin. The skin was disinfected with 70% ethanol prior to electrode attachment. The connecting cables were buried within the plumage

Table 1. Body mass, heart rate and time budget at sea of individual black-browed albatrosses

Bird ID	Body mass (kg)	Year	Recorder	Heart rate (beats min ⁻¹)				Time spent in each activity (%)				Time spent flapping (%)			
				Takeoff	Flapping in cruising flight	Gliding in cruising flight	Landing	On water	Takeoff	Cruising flight	Landing	On water	Takeoff	Cruising flight	
BBA1	3.70	2005	Heave & Activity							12.2 (494)	48.1 (1947)	10.2 (414)	29.4 (1191)	11.6	5.0
BBA2	3.40	2005	Heave & Activity							16.8 (399)	25.7 (610)	13.1 (312)	44.3 (1052)	7.3	4.6
BBA4	3.05	2005	Heave & Activity							13.0 (378)	64.6 (1884)	9.1 (266)	13.3 (387)	8.6	5.5
BBA5	3.45	2005	Heave & Activity							13.2 (534)	49.4 (1999)	7.2 (293)	30.2 (1221)	5.8	3.4
BBA6	3.65	2009	Heave							10.0 (218)	57.0 (1241)	6.9 (150)	26.2 (570)	9.2	5.6
BBA7	4.17	2009	ECG & Heave	200.0±63.1 (105)	158.6±36.1 (107)	137.1±15.4 (83)	186.5±55.9 (121)	134.1±26.3 (278)	11.7 (164)	32.0 (449)	13.4 (188)	42.9 (603)	13.2	5.4	
BBA8	4.25	2009	ECG & Heave	217.9±72.1 (32)	159.5±26.0 (229)	125.4±14.7 (142)	189.0±48.7 (65)	143.7±37.2 (159)	7.6 (174)	54.1 (1232)	8.2 (186)	30.1 (687)	15.9	5.7	
BBA9	3.60	2009	ECG & Heave	240.3±87.2 (50)	157.0±58.0 (56)	130.4±19.3 (168)	210.3±37.5 (75)	171.5±28.2 (82)	8.9 (187)	61.6 (1290)	9.4 (196)	20.1 (422)	6.9	1.7	
Mean	3.66±0.40								11.7±2.9	49.1±13.8	9.7±2.5	29.6±10.4	9.8±3.5	4.6±1.4	

Means are presented ±s.d. Numbers in parentheses indicate recording duration in min. Year is the year when the birds were instrumented. The recorders used included an electrocardiogram recorder (ECG), accelerometer (Heave) and activity logger (Activity). Heart rates were calculated every minute and classified into activity phases (see Materials and methods for definitions). The cruising flight phase for heart rate was divided into flapping and gliding phases. When calculating the heart rate, the flapping phase was identified when the bird flapped more than once a minute. During the flapping phase, birds spent 8.3–16.3% of the time flapping on average (14–28 flaps min⁻¹). Times spent in each activity are presented as the percentages of the whole period at sea. Time spent flapping indicates the percentage of time spent flapping when a bird is flying.

and held in place with waterproof tape. The logger was attached on the centre of the back of each bird with Tesa tape (Beiersdorf AG, Hamburg, Germany). Once the ECG recorder was attached, we confirmed the reliability of the recorded signal using an ECG monitor (HeartMate IEC-11103; Nihon-Koden, Tokyo, Japan). A start timer was used to delay the onset of recording, so that the ECG recorder began monitoring 3 or 6 h after deployment to allow for any time spent at the nest and any potential influence of handling stress (Weimerskirch et al., 2002). Upon removal of the electrodes when the bird was recaptured, antibiotic ointment (gentamicin; Schering-Plough, Osaka, Japan) was administered at the electrode insertion points. The recorded periods during foraging were 7.2, 10.5 and 11.6 h, respectively.

The accelerometer (M-190-D2GT; Little Leonardo) was 15 mm in diameter and 53 mm in length, and had a mass of 18 g in air. It recorded temperature (sampling frequency, 1 Hz), depth (sampling frequency, 1 Hz) and two-dimensional acceleration (sampling frequency, 16 or 32 Hz), surging along the longitudinal axis of the birds and heaving along the dorsoventral axis. Only the heaving axis data were used in this study as these reliably provide an indication of flapping. The logger was attached to the centre of the back of the bird with Tesa tape. The recording durations were 23–68 h.

The activity recorder (9 g, GLS-Mk3, British Antarctic Survey) (Afanasyev, 2004) was used to measure activity patterns (sitting on water or flying), and was fitted on the tarsus using a plastic leg band. Every 3 s, it recorded whether it was submerged in seawater or in air, storing the sum of the time that it was submerged in seawater at the end of each 10-min period. Recorded values ranged between 0 and 200, such that a value of 0 indicated that the logger was always dry, and 200 indicated that the logger was always wet. The recording duration covered the entire foraging trip.

The total mass of the combination of the recorders was ~1% of the body mass, which was assumed to be small enough to cause no severe behavioural disruptions (e.g. Phillips et al., 2003).

Data analysis

Although we had confirmed the reliability of the ECG signal at the attached recorder (Fig. 1), the baseline of the ECG signal sometimes fluctuated when birds flapped. In the worst case, only the R-wave could be identified in the ECG signal. The frequency of the fluctuation that was associated with flapping was longer than that of the R-wave in the ECG signal. Thus, the ECG records were filtered using a purpose-written programme (IGOR Pro version 6.1; WaveMetrics, Lake Oswego, OR, USA) to remove noise caused by muscular movements. Subsequently, we calculated the heart rate every minute.

Behavioural data analysis was performed using IGOR Pro with the program package Ethographer (Sakamoto et al., 2009a). The time series data were categorised based on the characteristics of the heave acceleration signal to discriminate behavioural patterns. Heave acceleration is modulated by dynamic motion along the dorsoventral

axis, such as flapping behaviour. We employed the method of Sakamoto et al. (Sakamoto et al., 2009a) to characterise the acceleration signal. Briefly, heave acceleration was converted to a spectrogram by continuous wavelet transformation using the Morlet mother wavelet with a non-dimensional frequency of 10 (Fig. 2A). The analysis time bin of the spectrogram was set to 2 s. The spectrogram was examined at 24 time steps with a periodicity range of 0.20–5.0 s, which included both flapping and soaring behaviours of albatrosses (Sato et al., 2009). Twenty-four time steps of examining the periodicity were confirmed to provide sufficient resolution to describe the motion of the birds. After generating the spectrogram, those from eight birds were combined and processed by the *k*-means clustering algorithm to discriminate behavioural patterns. The cluster number was set to 10, as higher cluster numbers artificially separated highly similar spectra that represented the same behaviour. The centroids of the clusters indicated the typical behaviour patterns and were represented as the spectra of dynamic motion (Fig. 2B–E). The 10 generated spectra could be classified into four groups. The first group showed a high amplitude at a cycle of *ca.* 0.35 s, which corresponds to flapping frequency (Sato et al., 2009) and indicates flapping behaviour (Fig. 2B). The second group was characterised as low amplitude over the entire range of the cycle, indicating stationary behaviour such as resting on water (Fig. 2C). The third group was characterised as a combination of low-amplitude 0.20–1.0 s cycles and high-amplitude 1.0–5.0 s cycles, which corresponded to soaring behaviour (Fig. 2D) (see Sato et al., 2009). The fourth group showed high amplitude in all cycle ranges, suggesting strong dynamic movement of the torso, although actual behaviour could not be identified (Fig. 2E). This type of behaviour appeared spontaneously and comprised only $0.17 \pm 0.15\%$ (mean \pm s.d., $N=8$) of the recorded time. Thus, we excluded this type of behaviour from further analysis.

Next, we identified whether a bird was in flight or on water based on the time series sequence of the categorised behaviour groups. A flying bird should show flapping or gliding behaviour (the first or third behaviour group), whereas a bird sitting on water should show resting behaviour (the second behaviour group). As the spectrogram bins were 2 s, the categorised behaviours represented motion for 2 s. Considering a 1-min block for a behaviour sequence, the major parts of the sequences were characterised by a continuous record of resting behaviour ($21.1 \pm 9.1\%$ of the entire time; mean \pm s.d., $N=8$; Fig. 2C) or a complete lack of resting behaviour ($46.6 \pm 11.6\%$ of the entire time; $N=8$). The combination of both types of behaviour comprised $67.6 \pm 6.0\%$ ($N=8$) of the time. A bird was defined as sitting on water when a 1-min block showed resting behaviour of >20 s. The other part was defined as the bird in flight.

Behavioural discrimination by the method of Sakamoto et al. (Sakamoto et al., 2009a) is a relatively new technique and our data allowed the method to be validated. For this, we compared the activity patterns of every 10-min block determined by both heave acceleration and the activity logger from the four birds equipped

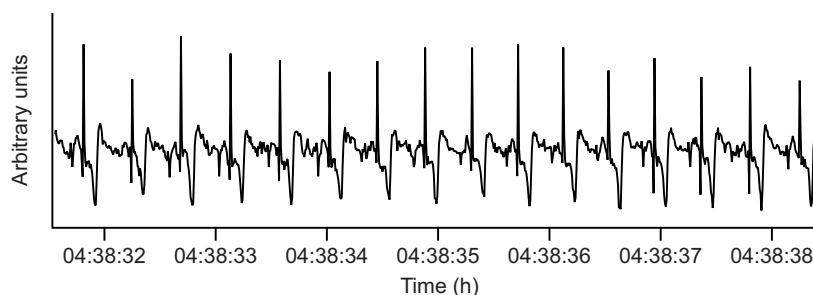


Fig. 1. Representative electrocardiogram of the black-browed albatross. Peaks in the trace indicate R-waves.

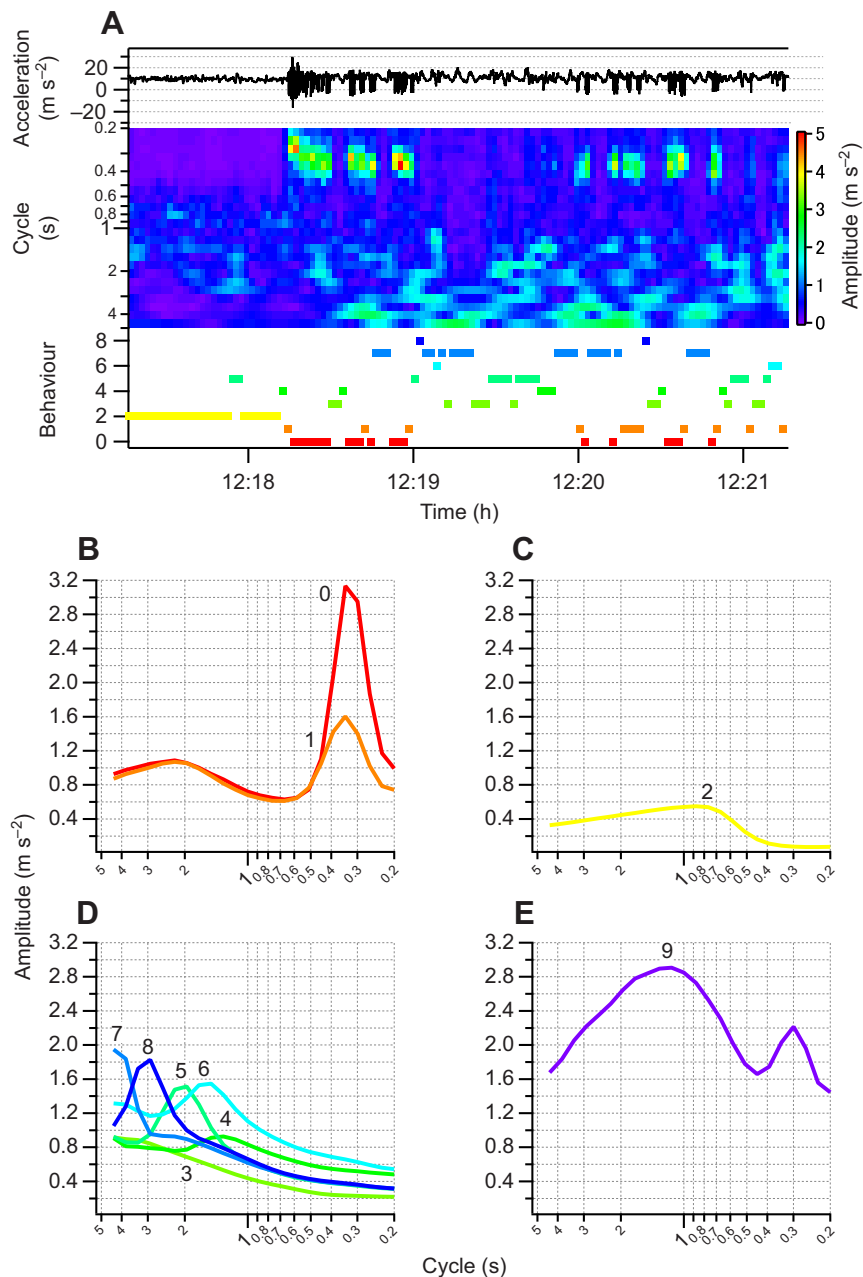


Fig. 2. Behavioural discrimination by the body acceleration signal from black-browed albatrosses and the discrete behaviour spectra. (A) Heave acceleration (black line, top) was converted into a spectrogram (middle) by continuous wavelet transformation. Ten discrete behaviours assigned to each time point were determined by the spectrogram characteristics (bottom). In the trace, the bird took off at 12:18 h and continued to fly. The large amplitude in the spectrogram at takeoff indicates flapping activity and was assigned a behavioural element of 0 and 1. The spectra of the behaviour indicate (B) flapping, (C) resting on water, (D) soaring and (E) strong dynamic movement. The numbers on the spectra correspond to the behaviour identification indicated at the bottom of Fig. 2A.

with both recorders. In the case of the activity recorder, a flight bout was defined as a 10-min block during which the bird spent >570 s (95% of the time) in a dry condition, with a wet bout defined for the remaining time. A flight bout for heave acceleration was defined as a continuous sequence of a 1-min block of flight for 10 min, and a wet bout was defined as the remaining time. Although measurement by both methods may result in error and noise, the activity patterns determined by both methods coincided well ($96.2 \pm 1.3\%$; mean \pm s.d., $N=4$). Thus, we assumed that discrimination using heave acceleration would be reliable.

The heart rate increases for 15–20 min at takeoff and landing in wandering albatrosses (*Diomedea exulans*) (Weimerskirch et al., 2000). We discriminated the takeoff and landing phases from the steady-state phase. Ten minutes from the onset of flight was defined as takeoff and 10 min from the onset of sitting on water was defined as landing. In cases in which the duration of flight or sitting on water was less than 10 min, the whole period was included in the takeoff or landing phase.

As is shown in Fig. 2A, the intensity of heave acceleration on the torso caused by flapping was always similar. However, because a flap took 0.35 s and albatrosses flapped several times in one session, the time spent flapping in each spectrogram bin (2 s) was variable. When a bird spent an equal amount of time flapping and gliding, the derived amplitude in the spectrogram would be half the amplitude for the period of full flapping activity. In Fig. 2B, the amplitudes of the dominant cycles of the spectra for flapping were 3.1 (spectrum 0) and 1.6 m s^{-2} (spectrum 1), respectively. This difference seemed to be derived from the duration of flapping in each spectrogram bin. The bird spent 2 s flapping at the moment of spectrum 0, whereas it spent 1 s flapping at the moment of spectrum 1. Thus, we calculated the time spent flapping every minute as the number of time points that were assigned to spectrum 0 or 1.

To examine the relationship between heart rate and activity, activity phase and time spent flapping during flight were determined for each 1-min block. Then we assigned mean heart rate values to continuous 1-min blocks of activity. We examined the relationship

between heart rate and time spent flapping on the data points derived from each 1-min block within the time series.

To avoid problems with pseudoreplication by repeated measurements from individual birds, linear mixed models using restricted maximum likelihood were used to estimate heart rate among the activity phases and the influence of flapping on heart rate. Bird identity was considered to be a random factor. We used R 2.14.2 (R Development Core Team, 2012) with the lmer function in R package lme4 for model fitting (Bates et al., 2011), and 95% confidence intervals (CI) and *P*-values of each parameter were obtained from 10,000 Markov chain Monte Carlo runs using the pvals.fnc function in the R package languageR (Baayen, 2011). To compare the time spent flapping between takeoff and cruising flight, we used a paired *t*-test. In all analyses, *P*<0.05 was taken to indicate statistical significance.

RESULTS

Typical traces of the time spent flapping and heart rate during a foraging trip are shown in Fig. 3. Heart rate was generally stable and low when a bird stayed on the water or flew for a long period of time, whereas heart rate increased during and shortly after takeoff and landing. During flight, the increase in heart rate was associated with flapping.

The estimated heart rates varied among different bird activities: 218 beats min⁻¹ (95% CI=157–286) for takeoff, 144 beats min⁻¹ (95% CI=118–173) for cruising flight, 195 beats min⁻¹ (95% CI=145–243) for landing and 150 beats min⁻¹ (95% CI=117–184) for sitting on water (Table 1, Fig. 4). The heart rates during takeoff and landing were significantly higher than those during steady phases, i.e. during cruising flight (95% CI of the difference=63–77, *P*<0.001) and on water (95% CI of the difference=42–53, *P*<0.001). Although heart rate increased significantly with increasing time spent flapping during takeoff (95% CI of the slope=3.0–5.0, *P*<0.01; Fig. 5A), the relationship was not strong (95% CI of the intercept=115–262). The major portion of the variation seemed to coincide with periods of high heart rate, implying that both flapping and other factors led to increased heart rates. In contrast, heart rate during cruising flight was linearly correlated with time spent flapping (95% CI of the slope=3.1–3.5, 95% CI of the intercept=100–169, *P*<0.01 for both; Fig. 5B). The estimated regression equation was:

$$f_H = 3.278T_f + 131.8, \quad (1)$$

where f_H is heart rate in beats min⁻¹ and T_f is time spent flapping in s min⁻¹. When a bird did not flap (i.e. gliding), its estimated heart rate was 131.8±2.8 beats min⁻¹ (mean ± s.e.m.).

The time budget was calculated for birds at sea (Table 1). Birds spent 60.7±12.2% (mean ± s.d., *N*=8) of their time flying (including both takeoff and cruising flight phases) and 39.3±12.2% sitting on water. Takeoff represented 11.7±2.9% of the time budget, whereas 49.1±13.8% of time was spent in cruising flight. Note that the takeoff phase included the whole flight period if flight continued for less than 10 min. Time spent flapping was calculated as the proportion of flapping time to total flying time. Flapping during cruising flight accounted for 4.6±1.4% of the flying time (range 1.7–5.7%), and was significantly lower than that during takeoff (9.8±3.5%, *P*<0.01).

DISCUSSION

We have provided the first continuous recording of flapping activity during albatross flight across the open ocean with simultaneous measurement of heart rate. During cruising flight, the heart rate of black-browed albatrosses was almost the same as that while sitting on water, whereas heart rates during takeoff and landing were much higher (Table 1, Figs 3, 4), indicating that the locomotion of flying was energetically similar to remaining on the sea surface. This finding was consistent with those of other studies that measured heart rate in free-ranging black-browed albatrosses and wandering albatrosses (Bevan et al., 1995; Weimerskirch et al., 2000). In addition, Shaffer et al. (Shaffer et al., 2001) estimated the field metabolic rate of wandering albatrosses using the doubly labelled water method and concluded that the number of takeoffs and landings explained the greatest proportion of variation in energy expenditure during a foraging trip. Black-browed albatrosses may sometimes feed on food scraps left by marine predators such as killer whales (*Orcinus orca*) (Sakamoto et al., 2009b). While foraging, albatrosses follow predators and repeatedly land on the sea surface. In the present study, heart rate during and shortly after landing was higher than when sitting on water. The high heart rate during and shortly after landing might have been due to feeding activity. Therefore, it seems reasonable that landing and takeoff, although energetically expensive, are essential parts of foraging (Green et al., 2009).

The heart rate of black-browed albatrosses was stable during gliding, suggesting that activities other than flapping do not require substantial additional energy during cruising flight (Fig. 5). In contrast, note that the increase in heart rate was only weakly related to flapping activity within 10 min of takeoff. In some cases, continuous flapping during takeoff would increase the heart rate, and the heart rate might remain high for a few minutes, which would result in a weak relationship with instantaneous flapping activity. Moreover, the variety of environmental conditions during takeoff might contribute to the large variation in heart rate during takeoff

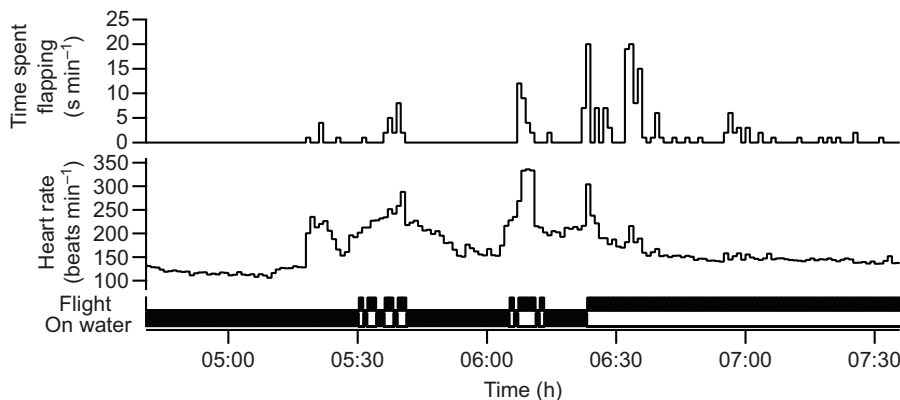


Fig. 3. Representative flapping activity and heart rate traces. The bottom part shows whether the bird was in flight or on water. The bird performed successive takeoffs and landings several times and then took off at 06:25 h for a prolonged flight.

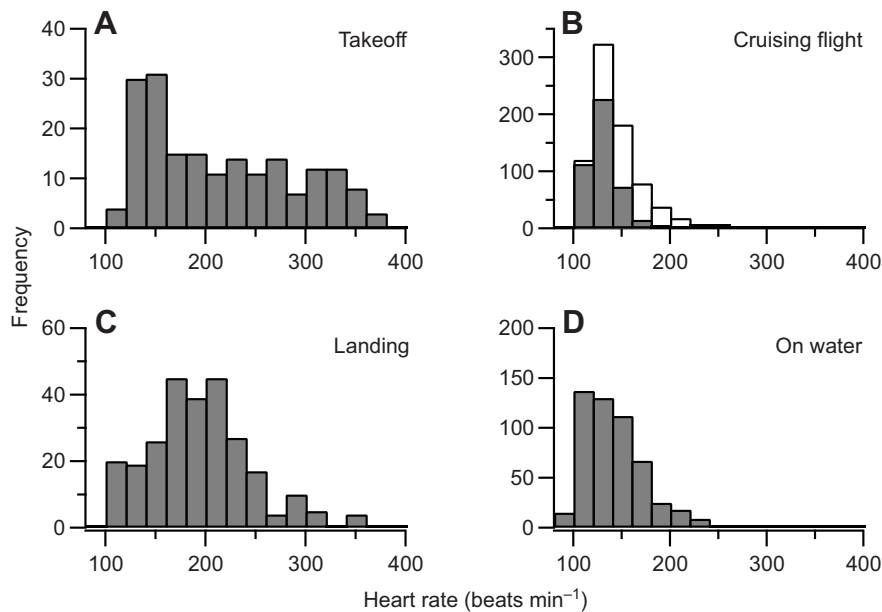


Fig. 4. Heart rate frequency distribution of black-browed albatrosses (A) at takeoff, (B) during cruising flight, (C) at landing and (D) sitting on water (three birds pooled). During cruising flight, heart rate is indicated by grey (when gliding) and white (when flapping more than once in a minute).

(e.g. condition of wind or water surface). However, according to the dorsoventral acceleration record, the heart rate increased occasionally even when the bird seemed to take off without running and started to glide immediately, indicating that the birds were performing some activity that did not appear in movement of the torso. Albatrosses are believed to lock their shoulder joints during flight (Pennycuik, 1982; Meyers and Stakebake, 2005). After the wing is moved forward to a fully protracted position, it is then resistant to being raised above the horizontal position. This mechanism is thought to reduce or eliminate the energy to strain the muscle for extending the wing, although it is unclear when albatrosses begin to apply the shoulder lock mechanism after takeoff. Thus, if albatrosses did not lock their wing at the beginning of the flight to adjust their flight mode to the ambient environment conditions, some energy may be used to keep the wing in the proper position (Baudinette and Schmidt-Nielsen, 1974; Goldspink et al., 1978). This energy consumption could explain the increased heart rate during takeoff, and would cause the weak relationship between heart rate and time spent flapping (Fig. 5A). Additional studies are

required to determine why heart rate increased even when the albatrosses' torsos did not move.

Black-browed albatrosses flapped for $4.6 \pm 1.4\%$ of the time during cruising flight. This proportion was consistent with previous observations from land and boats (Pennycuik, 1982) and was much lower than observations for red-footed boobies (*Sula sula*) in the open ocean [31.4–44.6% (Weimerskirch et al., 2005)]. The results of the present study indicate that flapping activity explains a major part of the heart rate increase during cruising flight (Fig. 5B). Flapping for 50% of the time during cruising flight (30 s min^{-1}) would account for a 75% increase in heart rate relative to the level during gliding. Although flight styles are different, these results are in contrast with those for Cape gannets. Gannets routinely alternate between flapping and gliding in flight (Ropert-Coudert et al., 2004). When gannets continue flapping flight for more than 1 min (i.e. flapping for 100% of time in flight), the elevation of heart rate from the level of gliding phase is only 20%, possibly due to the change in stroke volume in response to flight conditions (Ropert-Coudert et al., 2006).

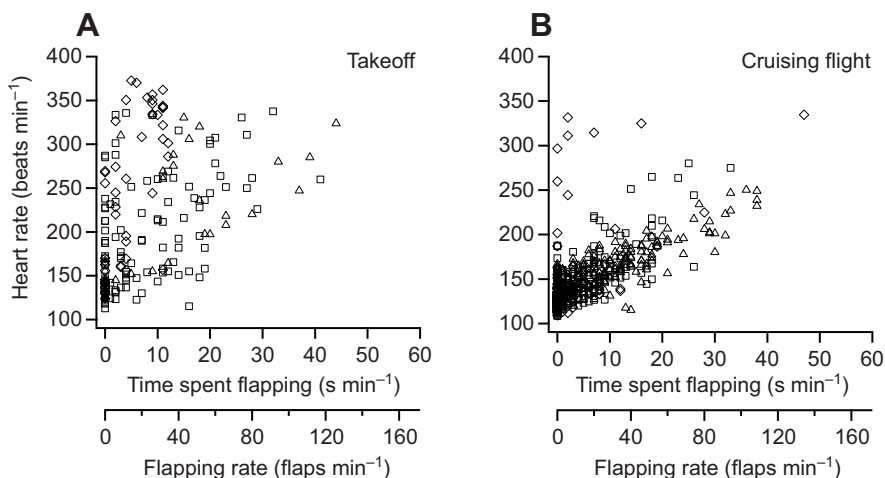


Fig. 5. Variation in heart rate in relation to time spent flapping (A) at takeoff and (B) during cruising flight. As the flapping frequency was constant (0.35 s for a flap), time spent flapping is converted into the number of flaps per minute. Individuals are discriminated by different markers ($N=3$).

The relationship between heart rate and the rate of oxygen consumption has been determined for black-browed albatrosses walking on a treadmill (Bevan et al., 1994; Bevan et al., 1995). The derived equation ($r^2=0.79$) was:

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

where \dot{V}_{O_2} is the rate of oxygen consumption in $\text{ml min}^{-1} \text{kg}^{-1}$. Assuming that 1 ml O_2 has an energy equivalent of 20.112 J (Bevan et al., 1995), the estimated energy expenditure values from the present study were 9.09 W kg^{-1} (takeoff), 4.66 W kg^{-1} (cruising flight), 7.60 W kg^{-1} (landing) and 4.98 W kg^{-1} (on water). By combining measurements of energy expenditure and time spent performing each activity, it is possible to estimate the energy required for a bird flying or sitting on water. On average, albatrosses spend 11.7% of each day performing takeoffs and 49.1% in cruising flight. In other words, takeoff accounted for 19.2% of flying time whereas cruising flight represented 80.8%. Therefore, the estimated energy expenditure for a flying bird would be 5.51 W kg^{-1} ($=9.09 \text{ W kg}^{-1} \times 19.2\% + 4.66 \text{ W kg}^{-1} \times 80.8\%$). In the same way, 5.62 W kg^{-1} would be required for a bird sitting on water (the period including both landing and on water phases). Our estimates are comparable with previous energy expenditure estimates that were created using the same relationship for this species when flying ($6.21 \pm 0.24 \text{ W kg}^{-1}$; mean \pm s.e.m.) and when on the water ($5.77 \pm 0.41 \text{ W kg}^{-1}$) (Bevan et al., 1995). Note that the error calculated as the standard error of the mean may be an underestimate in this context (Green, 2011) because the standard error of the mean ignores the error associated with variation in the relationship between heart rate and the rate of oxygen consumption.

The estimated energy expenditure during gliding was 4.04 W kg^{-1} , which was 1.7 times the energy expenditure when on the nest [$2.42 \pm 0.17 \text{ W kg}^{-1}$ (Bevan et al., 1995)]. The average additional energy expenditure for flapping could be estimated as the difference between the energy required for gliding and the average cruising flight. During cruising flight, albatrosses spent 4.6% of the time flapping and expended 4.66 W kg^{-1} on average. Therefore, 13.3% (0.62 W kg^{-1}) of the total energy spent during cruising flight would be expended for flapping.

As the number of flaps per minute was linearly correlated with heart rate during cruising flight, it was possible to estimate the energy expenditure for a flap. The difference in energy expenditure between a bird gliding and flapping for 10% of the time in cruising flight was 1.02 W kg^{-1} , which was equivalent to $60.9 \text{ J min}^{-1} \text{kg}^{-1}$. When the bird spent 10% of the time flapping, the bird flapped 17.1 times per minute because a single flap took 0.35 s. Therefore, albatrosses would expend $3.56 \text{ J kg}^{-1} \text{flap}^{-1}$ in addition to the energy required for gliding. Note that this estimation does not take into account the variance in flap style or wind condition during flight, which may have a significant influence on the energy expenditure for flapping. Although this was a rough estimate, it is of interest to compare with the values of $5.0 \text{ J kg}^{-1} \text{stride}^{-1}$ for trotting terrestrial mammals and $2.39 \text{ J kg}^{-1} \text{stroke}^{-1}$ for swimming seals (Heglund and Taylor, 1988; Kram and Taylor, 1990; Williams et al., 2004).

With respect to flight speed, the energy expenditure in general may be independent of ground speed during flight (Bevan et al., 1995). Albatrosses mainly move by soaring, which seemed to require a constant rate of oxygen consumption regardless of flight speed (Fig. 4B). However, when facing a head wind, wandering albatrosses fly at a low speed with a high heart rate, presumably because they spend more time flapping (Weimerskirch et al., 2000). Although 4.6% of the time during cruising flight was spent on flapping,

flapping could contribute to flight speed under certain conditions. Additional studies are needed to clarify this relationship.

In conclusion, we showed that flapping accounted for the major portion of the variation in energy expenditure during cruising flight. Black-browed albatrosses flapped for 4.6% of the time during cruising flight, but expended 13.3% of their energy on flapping, which supports the idea that birds perform energy-efficient cruising flight by reducing flapping activity, which requires high energy expenditures.

ACKNOWLEDGEMENTS

We would like to thank all the members of British Antarctic Survey (BAS) Bird Island Research Station 2005 and 2009 for their support during the fieldwork. We also thank J. A. Green, K. Taylor and two anonymous reviewers for providing valuable comments on the manuscript.

AUTHOR CONTRIBUTIONS

K.Q.S., A.T. and P.N.T. conceived and designed the study. K.Q.S., A.T., T.I. and M.Y. performed the experiments. K.Q.S. and T.Y. analyzed the data. K.Q.S. wrote the paper with input from all authors.

COMPETING INTERESTS

No competing interests declared.

FUNDING

This work was conducted as part of an international joint research project under the auspices of the Japanese Antarctic Research Expedition and the British Antarctic Survey during the International Polar Year, and was partially supported by a Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Science [22688023 to K.Q.S., 20310016 to A.T.].

REFERENCES

- Afanasyev, V. (2004). A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem. Natl. Inst. Polar Res.* **58 Special Issue**, 227-233.
- Baayen, R. H. (2011). *languageR: Data Sets and Functions With 'Analyzing Linguistic Data: A Practical Introduction to Statistics'*. R package version 1.4. Available at <http://cran.r-project.org/package=languageR>.
- Bates, D., Maechler, M. and Bolker, B. (2011). *lme4: Linear Mixed-Effects Models Using Eigen and S4*. R Package Version 0.999375-42. Available at <http://cran.r-project.org/package=lme4>.
- Baudinette, R. V. and Schmidt-Nielsen, K. (1974). Energy cost of gliding flight in herring gulls. *Nature* **248**, 83-84.
- Bevan, R. M., Woakes, A. J., Butler, P. J. and Boyd, I. (1994). The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys*. *J. Exp. Biol.* **193**, 119-137.
- Bevan, R. M., Butler, P. J., Woakes, A. J. and Prince, P. A. (1995). The energy expenditure of free-ranging black-browed albatrosses. *Philos. Trans. R. Soc. B* **350**, 119-131.
- Birt-Friesen, V. L., Montevecchi, W. A., Cairns, D. K. and Macko, S. A. (1989). Activity-specific rate of free-living northern gannets and other seabirds. *Ecology* **70**, 357-367.
- Butler, P. J., Woakes, A. J. and Bishop, C. M. (1998). Behaviour and physiology of Svalbard barnacle geese *Branta leucopsis* during their autumn migration. *J. Avian Biol.* **29**, 536-545.
- Butler, P. J., Green, J. A., Boyd, I. L. and Speakman, J. R. (2004). Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate method. *Funct. Ecol.* **18**, 168-183.
- Fick, A. (1870). Über die messung des blutquantums in den herzventrikeln. *Sitzungsber Phys. Med. Ges. Würzburg* **2**, 16. (In German).
- Goldspink, G., Mills, C. and Schmidt-Nielsen, K. (1978). Electrical activity of the pectoral muscles during gliding and flapping flight in the herring gull (*Larus argentatus*). *Experientia* **34**, 862-865.
- Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and recommendation. *Comp. Biochem. Physiol.* **158A**, 287-304.
- Green, J. A., White, C. R., Bunce, A., Frappell, P. B. and Butler, P. J. (2009). Energetic consequences of plunge diving in gannets. *Endanger. Species Res.* **10**, 269-279.
- Heglund, N. C. and Taylor, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318.
- Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.
- Meyers, R. A. and Stakebake, E. F. (2005). Anatomy and histochemistry of spreading posture in birds. 3. Immunohistochemistry of flight muscles and the 'shoulder lock' in albatrosses. *J. Morphol.* **263**, 12-29.
- Pelletier, D., Guillemette, M., Grandbois, J.-M. and Butler, P. J. (2008). To fly or not to fly: high flight costs in a large sea duck do not imply an expensive lifestyle. *Proc. Biol. Sci.* **275**, 2117-2124.
- Pennycuik, C. J. (1982). The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Philos. Trans. R. Soc. B* **300**, 75-106.

- Pennycuik, C. J.** (2002). Gust soaring as a basis for the flight of petrels and albatrosses (Procellariiformes). *Avian Sci.* **2**, 1-12.
- Phillips, R. A., Xavier, J. C. and Croxall, J. P.** (2003). Effects of satellite transmitters on albatrosses and petrels. *Auk* **100**, 1082-1090.
- R Development Core Team** (2012). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <http://www.R-project.org/>.
- Rayner, J.** (1977). The intermittent flight of birds. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 437-444. London: Academic Press.
- Richardson, P. L.** (2011). How do albatrosses fly around the world without flapping their wings? *Prog. Oceanogr.* **88**, 46-58.
- Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P. G., Naito, Y. and Le Maho, Y.** (2004). A fine-scale time budget of Cape gannets provides insights into their foraging strategies. *Anim. Behav.* **67**, 985-992.
- Ropert-Coudert, Y., Wilson, R. P., Grémillet, D., Kato, A., Lewis, S. and Ryan, P. G.** (2006). Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. *Mar. Ecol. Prog. Ser.* **328**, 275-284.
- Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S.** (2009a). Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* **4**, e5379.
- Sakamoto, K. Q., Takahashi, A., Iwata, T. and Trathan, P. N.** (2009b). From the eye of the albatrosses: a bird-borne camera shows an association between albatrosses and a killer whale in the Southern Ocean. *PLoS ONE* **4**, e7322.
- Sato, K., Daunt, F., Watanuki, Y., Takahashi, A. and Wanless, S.** (2008). A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *J. Exp. Biol.* **211**, 58-65.
- Sato, K., Sakamoto, K. Q., Watanuki, Y., Takahashi, A., Katsumata, N., Bost, C.-A. and Weimerskirch, H.** (2009). Scaling of soaring seabirds and implications for flight abilities of giant pterosaurs. *PLoS ONE* **4**, e5400.
- Shaffer, S. A.** (2011). A review of seabird energetics using the doubly labelled water method. *Comp. Biochem. Physiol.* **158A**, 315-322.
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H.** (2001). Behavioural factors affecting foraging effort of breeding wandering albatrosses. *J. Anim. Ecol.* **70**, 864-874.
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H.** (2004). Field metabolic rates of black-browed albatrosses *Thalassarche melanophrys* during the incubation stage. *J. Avian Biol.* **35**, 551-558.
- Tobalske, B. W.** (2007). Biomechanics of bird flight. *J. Exp. Biol.* **210**, 3135-3146.
- Videler, J. J.** (2005). *Avian Flight*. New York, NY: Oxford University Press.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. and Costa, D. P.** (2000). Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. Biol. Sci.* **267**, 1869-1874.
- Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P. and Jiraskova, S.** (2001). Energy saving in flight formation. *Nature* **413**, 697-698.
- Weimerskirch, H., Shaffer, S. A., Mabile, G., Martin, J., Boutard, O. and Rouanet, J. L.** (2002). Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *J. Exp. Biol.* **205**, 475-483.
- Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A. and Marsac, F.** (2005). The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proc. Biol. Sci.* **272**, 53-61.
- Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W.** (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973-982.
- Yamamoto, M., Kato, A., Ropert-Coudert, Y., Kuwahara, M., Hayama, S. and Naito, Y.** (2009). Evidence of dominant parasympathetic nervous activity of great cormorant (*Phalacrocorax carbo*). *J. Comp. Physiol.* **195**, 365-373.
- Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Le Maho, Y.** (2001). A new technique for monitoring the behaviour of free-ranging Adélie penguins. *J. Exp. Biol.* **204**, 685-690.