

1 **Title**

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

4
5 **Short title**

6 Energy cost of flight in albatrosses

7
8 **Authors and Affiliations**

9 Kentaro Q. Sakamoto^{1*}, Akinori Takahashi^{2, 3}, Takashi Iwata², Takashi Yamamoto³,
10 Maki Yamamoto⁴, Philip N. Trathan⁵

11
12 ¹Graduate School of Veterinary Medicine, Hokkaido University, Sapporo 060-0818,
13 Japan, ²Department of Polar Science, The Graduate University for Advanced Studies,
14 Tachikawa, Tokyo 190-8518, Japan, ³National Institute of Polar Research, Tachikawa,
15 Tokyo 190-8518, Japan, ⁴Department of Bioengineering, Nagaoka University of
16 Technology, Nagaoka 940-2188, Japan, ⁵British Antarctic Survey, Natural Environment
17 Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United
18 Kingdom.

19
20 * Corresponding author: Kentaro Q. Sakamoto

21 Tel. +81-11-706-5200; Fax. +81-11-706-5202

22 E-mail: sakamoto@vetmed.hokudai.ac.jp

23

24

25

26

SUMMARY

27 Albatrosses are known to expend only a small amount of energy during flight. The
28 low energy cost of albatross flight has been attributed to energy-efficient gliding
29 (soaring) with sporadic flapping, although little is known about how much time
30 and energy albatrosses expend in flapping versus gliding during cruising flight.
31 Here, we examined the heart rates (used as an instantaneous index of energy
32 expenditure) and flapping activities of free-ranging black-browed albatrosses
33 (*Thalassarche melanophrys*) to estimate the energy cost of flapping as well as time
34 spent in flapping activities. The heart rate of albatrosses during flight (144
35 beats min⁻¹) was similar to that while sitting on the water (150 beats min⁻¹). In
36 contrast, heart rate was much higher during takeoff and landing (*ca.* 200
37 beats min⁻¹). Heart rate during cruising flight was linearly correlated with the
38 number of wing flaps per minute, suggesting an extra energy burden of flapping.
39 Albatrosses expend only 4.6% ± 1.4% of their time in flapping during cruising
40 flight, which was significantly lower than those during and shortly after takeoff
41 (9.8% ± 3.5%). Flapping activity, which amounted to just 4.6% of the time in flight,
42 accounted for 13.3% of the total energy expenditure during cruising flight. These
43 results support the idea that albatrosses achieve energy-efficient flight by reducing
44 the time spent in flapping activity, which is associated with high energy
45 expenditure.

46

47

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

50

51

INTRODUCTION

52

53 Flapping activity is considered one of the major contributors to energy expenditure
54 during flight. Hence, many birds try to save energy by reducing the amount of flapping
55 (Videler, 2005; Tobalske, 2007). Birds employ diverse flight styles, including
56 intermittent flight, formation flight, and soaring (Rayner, 1977; Pennycuick, 2002;
57 Weimerskirch et al., 2004). Albatrosses provide a notable example of how birds reduce
58 energy expenditure during flight, as they have the lowest energy cost of transport by
59 unit mass and distance of all bird species examined to date (Videler, 2005). Albatrosses
60 have several features that allow such low-cost flight. The high aspect ratio of their
61 wings enables prolonged gliding until they lose altitude (Pennycuick, 1982). Moreover,
62 these birds use a soaring technique that extracts power for flight from ambient wind
63 over waves during gliding (Pennycuick, 2002; Richardson, 2011).

64 To better understand the efficiency of their low-cost flight, assessing how much
65 energy and time seabirds expend flapping and gliding during flight is essential, but few
66 studies have examined this issue. A previous study yielded somewhat surprising results,
67 as Cape gannet *Morus capensis* showed an increase in heart rate of only 20% during
68 flapping flight compared with gliding (Ropert-Coudert et al., 2006). More data on
69 energy cost of flapping for prolonged gliders such as albatrosses would provide new
70 insight into their unique style of flight. In addition, with the exception of observations
71 from land and boats (Pennycuick, 1982), there have been few reports regarding the time
72 spent flapping by albatrosses in the open ocean (Sato et al., 2009). Thus, to understand

73 flight costs under natural conditions, it is necessary to monitor both energy expenditure
74 and flapping activity simultaneously.

75 The energy expenditure of pelagic seabirds during flight has been estimated using
76 doubly labelled water and heart rate recording techniques. The doubly labelled water
77 technique measures the energy expenditure through the turnover of stable oxygen and
78 hydrogen isotopes in the blood, which reflect metabolic rate. The limitation of this
79 technique is that it provides only a single energy expenditure value over the entire
80 monitoring period. Several studies that applied the doubly labelled water technique
81 simultaneously recorded whether the bird was in flight or on water and estimated the
82 proportion of time spent in flight to determine the cost of flight (Birt-Friesen et al.,
83 1987; Shaffer, 2011; Shaffer et al., 2001; Shaffer et al., 2004). Another technique, heart
84 rate monitoring, measures the heart rate of the bird continuously during flight (Bevan et
85 al., 1995; Butler et al., 1998; Pelletier et al., 2008). Heart rate can reflect the rate of
86 oxygen consumption when both the stroke volume of the heart and the extraction of
87 oxygen by the body tissues change in a systematic fashion (Fick, 1870). Although these
88 values may change and thus the relationship may not be linear, heart rate is correlated
89 with the rate of oxygen consumption under most conditions (Butler et al., 2004; Green
90 et al., 2009; Green, 2011). Thus, once the relationship between heart rate and the rate of
91 oxygen consumption is established, properly calibrated and validated, heart rate can
92 serve as a good indicator of energy expenditure. The advantage of this technique is the
93 fine-scale, temporal resolution of the records.

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

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

115

116

117

MATERIALS AND METHODS

118

Fieldwork

119

Fieldwork was conducted at a black-browed albatross breeding colony on Bird Island

120

(54°00'S, 38°03'W), South Georgia, in January 2005 and 2009, which corresponded to

121

the chick-guarding period. This study was approved by the British Antarctic Survey and

122

the University of Cambridge Animal Ethics Board prior to the commencement of

123

fieldwork.

124

We equipped eight chick-rearing albatrosses at their nest sites; they were weighed

125

and equipped with recorders (Table 1). The masses of the birds ranged from 3.05 to

126

4.25 kg. Three birds had both an ECG recorder and an accelerometer attached (see

127

below), four birds had an accelerometer and an activity recorder attached and one bird

128

had only an accelerometer attached. Animal handling times were always <30 min and

129

all birds returned to the nest immediately after release before voluntarily departing on a

130

foraging trip. Instrumented birds were recaptured after a single foraging trip lasting 3–4

131

days; all recorders were retrieved and data were downloaded. The timing of arrival at

132

the nest could be easily identified from the acceleration data. Acceleration data recorded

133

at the nest were omitted, and only the data during the actual foraging trip were used for

134

analysis.

135

Instruments

136

137 The ECG recorder (UME-190-ECG; Little Leonardo Ltd., Tokyo, Japan) was 15 mm in
138 diameter and 73 mm in length, with a mass of 24 g in air, and was used to measure heart
139 rate (sampling frequency, 128 Hz). The recorder was composed of a data logger and
140 three disposable electrodes connected to the logger with cables. Two of the electrodes
141 were placed above and below the central part of the sternum to detect the electric
142 potential difference, while the third electrode was placed on the back of the bird to act
143 as a ground wire to reduce electrical noise (Yamamoto et al., 2009). All electrodes were
144 made of gold-plated safety pins and were placed under the skin. The skin was
145 disinfected with 70% ethanol prior to electrode attachment. The connecting cables were
146 buried within the plumage and held in place with waterproof tape. The logger was
147 attached on the centre of the back of each bird with Tesa tape (Beiersdorf AG, Hamburg,
148 Germany). Once the ECG recorder was attached, we confirmed the reliability of the
149 signal recorded using an ECG monitor (HeartMate IEC-11103; Nihon-Koden, Tokyo,
150 Japan). A start timer was used to delay the onset of recording, so that the ECG recorder
151 began monitoring 3 or 6 h after deployment to allow for any time spent at the nest and
152 any potential influence of handling stress (Weimerskirch et al., 2002). Upon removal of
153 the electrodes when the bird was recaptured, antibiotic ointment (gentamicin;
154 Schering-Plough, Osaka, Japan) was administered at the electrode insertion points. The
155 recorded periods during foraging were 7.2 h, 10.5 h and 11.6 h, respectively.

156 The accelerometer (M-190-D2GT; Little Leonardo Ltd.) was 15 mm in diameter and
157 53 mm in length, and had a mass of 18 g in air. It recorded temperature (sampling
158 frequency, 1 Hz), depth (sampling frequency, 1 Hz) and two-dimensional acceleration
159 (sampling frequency, 16 or 32 Hz), surging along the longitudinal axis of the birds and
160 heaving along the dorsoventral axis. Only the heaving axis data were used in this study
161 as these reliably provide an indication of flapping. The logger was attached to the centre
162 of the back of the bird with Tesa tape. The recording durations were 23–68 h.

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

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

173

174

Data analysis

175 Although we had confirmed the reliability of the EGC signal at the attached recorder
176 (Fig. 1), the baseline of the ECG signal sometimes fluctuated when birds flapped. In the

177 worst case, only the R-wave could be identified in the ECG signal. The frequency of the
178 fluctuation that was associated with flapping was longer than that of the R-wave in the
179 ECG signal. Thus, the ECG records were filtered using a purpose-written programme
180 (IGOR Pro ver. 6.1; WaveMetrics, Lake Oswego, OR, USA) to remove noise caused by
181 muscular movements. Subsequently, we calculated the heart rate every minute.

182 Behavioural data analysis was performed using IGOR Pro with the programme
183 package, Ethographer (Sakamoto et al., 2009a). The time series data were categorised
184 based on the characteristics of the heave acceleration signal to discriminate behavioural
185 patterns. Heave acceleration is modulated by dynamic motion along the dorsoventral
186 axis, such as flapping behaviour. We employed the method of Sakamoto et al. (2009a)
187 to characterise the acceleration signal. Briefly, heave acceleration was converted to a
188 spectrogram by continuous wavelet transformation using the Morlet mother wavelet
189 with a non-dimensional frequency of 10 (Fig. 2A). The analysis time bin of the
190 spectrogram was set to 2 s. The spectrogram was examined at 24 time steps with a
191 periodicity range of 0.20–5.0 s, which included both flapping and soaring behaviours of
192 albatrosses (Sato et al., 2009). Twenty-four time steps of examining the periodicity were
193 confirmed to provide sufficient resolution to describe the motion of the birds. After
194 generating the spectrogram, those from eight birds were combined and processed by the
195 *k*-means clustering algorithm to discriminate behavioural patterns. The cluster number
196 was set to 10, as higher cluster numbers artificially separated highly similar spectra that
197 represented the same behaviour. The centroids of the clusters indicated the typical

198 behaviour patterns and were represented as the spectra of dynamic motion (Fig. 2B–E).
199 The 10 generated spectra could be classified into four groups. The first group showed a
200 high amplitude at *ca.* 0.35 s cycle, which corresponds to flapping frequency (Sato et al.,
201 2009) and indicates flapping behaviour (Fig. 2B). The second group was characterised
202 as low amplitude over the entire range of the cycle, indicating stationary behaviour such
203 as resting on water (Fig. 2C). The third group was characterised as a combination of low
204 amplitude 0.20–1.0 s cycles and high amplitude 1.0–5.0 s cycles, which corresponded to
205 soaring behaviour (Fig. 2D) (see Sato et al., 2009). The fourth group showed high
206 amplitude in all cycle ranges, suggesting strong dynamic movement of the torso,
207 although actual behaviour could not be identified (Fig. 2E). This type of behaviour
208 appeared spontaneously and comprised only $0.17\% \pm 0.15\%$ (mean \pm s.d., $n = 8$) of the
209 recorded time. Thus, we excluded this type of behaviour from further analysis.

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

219 8) of the time. A bird was defined as sitting on water when a 1-min block showed
220 resting behaviour of >20 s. The other part was defined as the bird in flight.

221 Behavioural discrimination by the method of Sakamoto et al. (2009a) is a relatively
222 new technique and our data allowed the method to be validated. For this, we compared
223 the activity patterns of every 10-min block determined by both heave acceleration and
224 the activity logger from the four birds equipped with both recorders. In the case of the
225 activity recorder, a flight bout was defined as a 10-min block, during each of which the
226 bird spent >570 s (95% of the time) in a dry condition, and a wet bout was defined for
227 the remaining time. A flight bout for heave acceleration was defined as a continuous
228 sequence of a 1-min block of flight for 10 min, and a wet bout was defined as the
229 remaining time. Although measurement by both methods may result in error and noise,
230 the activity patterns determined by both methods coincided well ($96.2\% \pm 1.3\%$; mean
231 \pm s.d., $n = 4$). Thus, we assumed that discrimination using heave acceleration would be
232 reliable.

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

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

250 To examine the relationship between heart rate and activity, activity phase and time
251 spent flapping during flight were determined for each 1-min block. Then we assigned
252 mean heart rate values to continuous 1-min blocks of activity. We examined the
253 relationship between heart rate and time spent flapping on the data points derived from
254 each 1-min block within the time series.

255 To avoid problems with pseudoreplication by repeated measurements from
256 individual birds, linear mixed models using restricted maximum likelihood were used to
257 estimate heart rate among the activity phases and the influence of flapping on heart rate.
258 Bird identity was considered a random factor. We used R 2.14.2 (R Development Core
259 Team, 2012) with the lmer function in R package lme4 for model fitting (Bates et al.,

260 2011), and 95% confidence intervals (CI) and P -values of each parameter were obtained
261 from 10,000 Markov chain Monte Carlo runs using the `pvals.fnc` function in R package
262 `languageR` (Baayen, 2011). To compare the time spent flapping between takeoff and
263 cruising flight, we used a paired t -test. In all analyses, $P < 0.05$ was taken to indicate
264 statistical significance.

265

266

267

RESULTS

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

273 The estimated heart rates varied among different bird activities: 218 beats min^{-1}
274 (95% CI, 157–286) for takeoff, 144 beats min^{-1} (95% CI, 118–173) for cruising flight,
275 195 beats min^{-1} (95% CI, 145–243) for landing and 150 beats min^{-1} (95% CI, 117–184)
276 for sitting on water (Table 1, Fig. 4). The heart rates during takeoff and landing were
277 significantly higher than those during steady phases: during cruising flight (95% CI of
278 the difference, 63–77, $P < 0.001$) and on water (95% CI of the difference, 42–53, $P <$
279 0.001). Although heart rate increased significantly with increasing time spent flapping
280 during takeoff (Fig. 5A; 95% CI of the slope, 3.0–5.0, $P < 0.01$), the relationship was

281 not strong (95% CI of the intercept, 115–262). The major portion of the variation
282 seemed to coincide with periods of high heart rate, implying that both flapping and
283 other factors led to increased heart rates. In contrast, heart rate during cruising flight
284 was linearly correlated with time spent flapping (Fig. 5B; 95% CI of the slope, 3.1–3.5;
285 95% CI of the intercept, 100–169, $P < 0.01$ for both). The estimated regression equation
286 was:

$$287 \quad f_H = 3.278T_f + 131.8 \quad (1),$$

288 where f_H is heart rate in beats min^{-1} and T_f is time spent flapping in s min^{-1} . When a bird
289 did not flap (i.e., gliding), its estimated heart rate was 131.8 ± 2.8 beats min^{-1} (mean \pm
290 s.e.m.).

291 The time budget was calculated for birds at sea (Table 1). Birds spent $60.7\% \pm$
292 12.2% (mean \pm s.d., $n = 8$) of their time flying (including both takeoff and cruising
293 flight phases) and $39.3\% \pm 12.2\%$ sitting on water. Takeoff represented $11.7\% \pm 2.9\%$
294 of the time budget, whereas $49.1\% \pm 13.8\%$ of time was spent during cruising flight.
295 Note that the takeoff phase included the whole flight period if flight continued for less
296 than 10 min. Time spent flapping was calculated as the proportion of flapping time to
297 total flying time. Flapping during cruising flight accounted for $4.6\% \pm 1.4\%$ of the
298 flying time (range 1.7–5.7%), and was significantly lower than that during takeoff
299 ($9.8\% \pm 3.5\%$, $P < 0.01$).

300

301

DISCUSSION

302

303 We have provided the first continuous recording of flapping activity during albatross
304 flight across the open ocean with simultaneous measurement of heart rate. During
305 cruising flight, the heart rate of black-browed albatrosses was almost the same as that
306 while sitting on water, whereas heart rates during takeoff and landing were much higher
307 (Table 1, Figs. 3, 4), indicating that the locomotion of flying was energetically similar
308 to remaining on the sea surface. This finding was consistent with those of other studies
309 that measured heart rate in free-ranging black-browed albatrosses and wandering
310 albatrosses (Bevan et al., 1995; Weimerskirch et al., 2000). In addition, Shaffer et al.
311 (2001) estimated the field metabolic rate of wandering albatrosses using the doubly
312 labelled water method and concluded that the number of takeoffs and landings
313 explained the greatest proportion of variation in energy expenditure during a foraging
314 trip. Black-browed albatrosses may sometimes feed on food scraps left by marine
315 predators such as killer whales (*Orcinus orca*; Sakamoto et al., 2009b). While foraging,
316 albatrosses follow predators and repeatedly land on the sea surface. In this study, heart
317 rate during and shortly after landing was higher than when sitting on water. The high
318 heart rate during and shortly after landing might have been due to feeding activity.
319 Therefore, it seems reasonable that landing and takeoff, although energetically
320 expensive, are essential parts of foraging (Green et al., 2009).

321 The heart rate of black-browed albatrosses was stable during gliding, suggesting that
322 activities other than flapping do not require substantial additional energy during cruising

323 flight (Fig. 5). In contrast, note that the increase in heart rate was only weakly related to
324 flapping activity within 10 min from takeoff. In some cases, continuous flapping during
325 takeoff would increase the heart rate, and the heart rate might remain high for a few
326 minutes, which would result in a weak relationship with instantaneous flapping activity.
327 Moreover, the variety of environmental conditions during takeoff might contribute to
328 the large variation in heart rate during takeoff (e.g. condition of wind or water surface).
329 However, according to the dorsoventral acceleration record, the heart rate increased
330 occasionally even when the bird seemed to take off without running and started to glide
331 immediately, indicating that the birds were performing some activity that did not appear
332 in movement of the torso. Albatrosses are believed to lock their shoulder joints during
333 flight (Pennycuick, 1982; Meyers and Stakebake, 2005). After the wing is moved
334 forward to a fully protracted position, it is then resistant to being raised above the
335 horizontal position. This mechanism is thought to reduce or eliminate the energy to
336 strain the muscle for extending the wing, although it is unclear when albatrosses begin
337 to apply the shoulder lock mechanism after takeoff. Thus, if albatrosses did not lock
338 their wing at the beginning of the flight to adjust their flight mode to the ambient
339 environment conditions, some energy may be used to keep the wing in the proper
340 position (Baudinette and Schmidt-Nielsen, 1974; Goldspink et al., 1978). This energy
341 consumption could explain the increased heart rate during takeoff, and would cause the
342 weak relationship between heart rate and time spent flapping (Fig. 5A). Additional

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

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

358 The relationship between heart rate and the rate of oxygen consumption has been
359 determined for black-browed albatrosses walking on a treadmill (Bevan et al., 1994,
360 1995). The derived equation was:

361
$$\dot{V}_{O_2} = 0.00466f_H^{1.61} \quad (r^2 = 0.79) \quad (2),$$

362 where \dot{V}_{O_2} is the rate of oxygen consumption in $\text{mL min}^{-1} \text{ kg}^{-1}$ and f_H is heart rate in
363 beats min^{-1} . Assuming that 1 mL O_2 has an energy equivalent of 20.112 J (Bevan et al.,

364 1995), the estimated energy expenditure values from the present study were 9.09 W kg^{-1}
365 (takeoff), 4.66 W kg^{-1} (cruising flight), 7.60 W kg^{-1} (landing) and 4.98 W kg^{-1} (on
366 water). By combining measurements of energy expenditure and time spent performing
367 each activity, it is possible to estimate the energy required for a bird flying or sitting on
368 water. On average, albatrosses spend 11.7% of each day performing takeoffs and 49.1%
369 in cruising flight. In other words, takeoff accounted for 19.2% of flying time whereas
370 cruising flight represented 80.8%. Therefore, the estimated energy expenditure for a
371 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
372 the same way, 5.62 W kg^{-1} would be required for a bird sitting on water (the period
373 including both landing and on water phases). Our estimates are comparable with
374 previous energy expenditure estimates that were created using the same relationship for
375 this species when flying ($6.21 \pm 0.24 \text{ W kg}^{-1}$; mean \pm s.e.m.) and when on the water
376 ($5.77 \pm 0.41 \text{ W kg}^{-1}$) (Bevan et al., 1995). Note that the error calculated as the standard
377 error of the mean may be an underestimate in this context (Green et al., 2011) because
378 the standard error of the mean ignores the error associated with variation in the
379 relationship between heart rate and the rate of oxygen consumption.

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

385 W kg⁻¹ on average. Therefore, 13.3% (0.62 W kg⁻¹) of the total energy spent during
386 cruising flight would be expended for flapping.

387 As the number of flaps per minute was linearly correlated with heart rate during
388 cruising flight, it was possible to estimate the energy expenditure for a flap. The
389 difference in energy expenditure between a bird gliding and flapping for 10% of the
390 time in cruising flight was 1.02 W kg⁻¹, which was equivalent to 60.9 J min⁻¹ kg⁻¹.
391 When the bird spent 10% of the time flapping, the bird flapped 17.1 times for 1 min
392 because a single flap took 0.35 s. Therefore, albatrosses would expend 3.56 J kg⁻¹ flap⁻¹
393 in addition to the energy required for gliding. Note that this estimation does not take
394 into account the variance in flap style or wind condition during flight, which may have a
395 significant influence on the energy expenditure for flapping. Although this was a rough
396 estimate, it is of interest to compare with the values of 5.0 J kg⁻¹ stride⁻¹ for trotting
397 terrestrial mammals and 2.39 J kg⁻¹ stroke⁻¹ for swimming seals (Heglund and Taylor,
398 1988; Kram and Taylor, 1990; Williams et al., 2004).

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

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

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

412

413

414

ACKNOWLEDGEMENTS

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

419

420

421

FUNDING

422 This work was conducted as part of an international joint research project under the
423 auspices of the Japanese Antarctic Research Expedition and the British Antarctic
424 Survey during the International Polar Year, and was partially supported by a

425 Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of

426 Science [22688023 to K. Q. S., 20310016 to A. T.].

427

428

429

REFERENCES

- 430
- 431 **Afanasyev, V.** (2004). A miniature daylight level and activity data recorder for tracking
432 animals over long periods. *Mem. Natl. Inst. Polar Res.*, Special Issue **58**, 227-233.
- 433 **Baayen, R. H.** (2011). languageR: data sets and functions with “analyzing linguistic
434 data: a practical introduction to statistics”. R package version 1.4.
435 <http://CRAN.R-project.org/package=languageR>.
- 436 **Bates, D., Maechler, M. and Bolker, B.** (2011). lme4: linear mixed-effects models
437 using S4 classes. R Package Version 0.999375-42
438 <http://CRAN.R-project.org/package=lme4>.
- 439 **Baudinette, R. V. and Schmidt-Nielsen K.** (1974). Energy cost of gliding flight in
440 herring gulls. *Nature* **248**, 83-84.
- 441 **Bevan, R. M., Woakes, A.J. and Butler, P. J.** (1994). The use of heart rate to estimate
442 oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys*.
443 *J. Exp. Biol.* **193**, 119-137.
- 444 **Bevan, R. M., Butler, P. J., Woakes, A. J. and Prince, P. A.** (1995). The energy
445 expenditure of free- ranging black-browed albatrosses. *Phil. Trans. R. Soc. Lond. B* **350**,
446 119-131.
- 447 **Birt-Friesen, V. L., Montevicchi, W. A., Cairns, D. K. and Macko, S. A.** (1987).
448 Activity-specific rate of free-living northern gannets and other seabirds. *Ecology* **70**,
449 357-367.
- 450 **Butler, P. J., Woakes, A. J. and Bishop C. M.** (1998). Behaviour and physiology of

451 Svalbard Barnacle Geese *Branta leucopsis* during their autumn migration. *J. Avian Biol.*
452 **29**, 536-545.

453 **Butler, P. J., Green, J. A., Boyd, I. L. and Speakman, J. R.** (2004). Measuring
454 metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate
455 method. *Funct. Ecol.* **18**, 168-183.

456 **Fick, A.** (1870). Über die Messung des Blutquantums in den Herzventrikeln.
457 *Sitzungsber Phys. Med. Ges. Würzburg* **2**, 16 (in German).

458 **Green, J. A.** (2011). The heart rate method for estimating metabolic rate: review and
459 recommendation. *Comp. Biochem. Physiol. A* **158**, 287-304.

460 **Green, J. A., White, C. R., Bunce, A., Frappell, P. B. and Butler, P. J.** (2009).
461 Energetic consequences of plunge diving in gannets. *Endang. Species Res.* **10**, 269-279.

462 **Goldspink, G., Mills, C. and Schmidt-Nielsen, K.** (1978). Electrical activity of the
463 pectoral muscles during gliding and flapping flight in the herring gull (*Larus*
464 *argentatus*). *Experimentia* **34**, 862-865.

465 **Heglund, N. C. and Taylor, R.** (1988). Speed, stride frequency and energy cost per
466 stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318.

467 **Kram, R. and Taylor, R.** (1990). Energetics of running: a new perspective. *Nature* **346**,
468 265-267.

469 **Meyers, R. A. and Stakebake, E. F.** (2005). Anatomy and histochemistry of
470 spread-wing posture in birds. 3. Immunohistochemistry of flight muscles and the
471 “shoulder lock” in albatrosses. *J. Morphol.* **263**, 12-29.

472 **Pelletier, D., Guillemette, M., Grandbois, J.-M. and Butler P. J.** (2008). To fly or
473 not to fly: high flight costs in a large sea duck do not imply an expensive lifestyle. *Proc.*
474 *R. Soc. B* **275**, 2117-2124.

475 **Pennycuik, C. J.** (1982). The flight of petrels and albatrosses (*Procellariiformes*),
476 observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. Lond. B* **300**, 75-106.

477 **Pennycuik, C. J.** (2002). Gust soaring as a basis for the flight of petrels and
478 albatrosses (*Procellariiformes*). *Avian Sci.* **2**, 1-12.

479 **Phillips, R. A., Xavier, J. C. and Croxall, J. P.** (2003). Effects of satellite transmitters
480 on albatrosses and petrels. *Auk* **100**, 1082-1090.

481 **Rayner, J.** (1977). The intermittent flight of birds. In *Scale Effects in Animal*
482 *Locomotion* (ed. T. J. Pedley), pp. 437-444. London: Academic Press.

483 **R Development Core Team** (2012). R: a language and environment for statistical
484 computing. R Foundation for Statistical Computing, Vienna, Austria.
485 <http://www.R-project.org/>.

486 **Richardson, P. L.** (2011). How do albatrosses fly around the world without flapping
487 their wings? *Prog. Oceanogr.* **88**, 46-58.

488 **Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P. G., Naito, Y. and Le Maho,**
489 **Y.** (2004). A fine-scale time budget of Cape gannets provides insights into their
490 foraging strategies. *Anim. Behav.* **67**, 985-992.

491 **Ropert-Coudert, Y., Wilson, R. P., Grémillet, D., Kato, A., Lewis, S. and Ryan, P.**
492 **G.** (2006). Electrocardiogram recordings in free-ranging gannets reveal minimum

493 difference in heart rate during flapping versus gliding flight. *Mar. Ecol. Prog. Ser.* **328**,
494 275-284.

495 **Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F.**
496 **and Wanless, S.** (2009a). Can ethograms be automatically generated using body
497 acceleration data from free-ranging birds? *PLoS ONE* **4**, e5379.

498 **Sakamoto, K. Q., Takahashi, A., Iwata, T. and Trathan, P. N.** (2009b). From the eye
499 of the albatrosses: a bird-borne camera shows an association between albatrosses and a
500 killer whale in the Southern Ocean. *PLoS ONE* **4**, e7322.

501 **Sato, K., Daunt, F., Watanuki, Y., Takahashi, A. and Wanless, S.** (2008). A new
502 method to quantify prey acquisition in diving seabirds using wing stroke frequency. *J.*
503 *Exp. Biol.* **211**, 58-65.

504 **Sato, K., Sakamoto, K. Q., Watanuki, Y., Takahashi, A., Katsumata, N., Bost, C.-A.**
505 **and Weimerskirch, H.** (2009). Scaling of soaring seabirds and implications for flight
506 abilities of giant Pterosaurs. *PLoS ONE* **4**, e5400.

507 **Shaffer, S. A.** (2011). A review of seabird energetics using the doubly labelled water
508 method. *Comp. Biochem. Physiol. A* **158**, 315-322.

509 **Shaffer, S. A., Costa, D. P. and Weimerskirch, H.** (2001). Behavioural factors
510 affecting foraging effort of breeding wandering albatrosses. *J. Anim. Ecol.* **70**, 864-874.

511 **Shaffer, S. A., Costa, D. P. and Weimerskirch, H.** (2004). Field metabolic rates of
512 black-browed albatrosses *Thalassarche melanophrys* during the incubation stage. *J.*
513 *Avian Biol.* **35**, 551-558.

514 **Tobalske, B. W.** (2007). Biomechanics of bird flight. *J. Exp. Biol.* **210**, 3135-3146.

515 **Videler, J. J.** (2005). *Avian Flight*. New York: Oxford University Press.

516 **Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. and Costa, D. P.** (2000).

517 Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. Lond. B*

518 **267**, 1869-1874.

519 **Weimerskirch, H., Shaffer, S. A., Mabile, G., Martin, J., Boutard, O. and Rouanet,**

520 **J. L.** (2002). Heart rate and energy expenditure of incubating wandering albatrosses:

521 basal levels, natural variation, and the effects of human disturbance. *J. Exp. Biol.* **205**,

522 475-483.

523 **Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P. and Jiraskova, S.** (2004).

524 Energy saving in flight formation. *Nature* **413**, 697-698.

525 **Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A. and Marsac, F.**

526 (2005). The three-dimensional flight of red-footed boobies: adaptations to foraging in a

527 tropical environment? *Proc. R. Soc. B* **272**, 53-61.

528 **Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W.** (2004). The cost of

529 foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the

530 stroke. *J. Exp. Biol.* **207**, 973-982.

531 **Yamamoto, M., Kato, A., Ropert-Coudert, Y., Kuwahara, M., Hayama, S. and**

532 **Naito, Y.** (2009). Evidence of dominant parasympathetic nervous activity of great

533 cormorant (*Phalacrocorax carbo*). *J. Comp. Physiol.* **195**, 365-373.

534 **Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y.,**

535 **Kurita, M. and Le Maho, Y.** (2001). A new technique for monitoring the behaviour of
536 free-ranging Adelie penguins. *J. Exp. Biol.* **204**, 685-690.

537

538

539

540 **Figure Legends**

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

543

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

554

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

558

559 Fig. 4. Heart rate frequency distribution of black-browed albatrosses (A) at takeoff, (B)
560 during cruising flight, (C) at landing and (D) sitting on water (three birds pooled).

561 During cruising flight, heart rate is indicated by grey (when gliding) and white (when
562 flapping more than once in a minute).

563

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

568

569

570

571 Table 1. Body masses, heart rates and time budget at sea of individual black-browed
572 albatrosses. Year is the year when the birds were instrumented. The recorders used
573 included an electrocardiogram recorder (ECG), accelerometer (Heave) and activity
574 logger (Activity). Heart rates were calculated every minute and classified into activity
575 phases (see Materials and methods for definitions). The cruising flight phase for heart
576 rate was divided into flapping and gliding phases. When calculating the heart rate, the
577 flapping phase was identified when the bird flapped more than once in a minute. During
578 the flapping phase, birds spent 8.3%–16.3% of the time flapping on average (14–28
579 flaps min^{-1}). Times spend in each activity are represented as the percentages of the
580 whole period at sea. Time spend flapping indicates the percentage of time spent flapping
581 when a bird is flying.

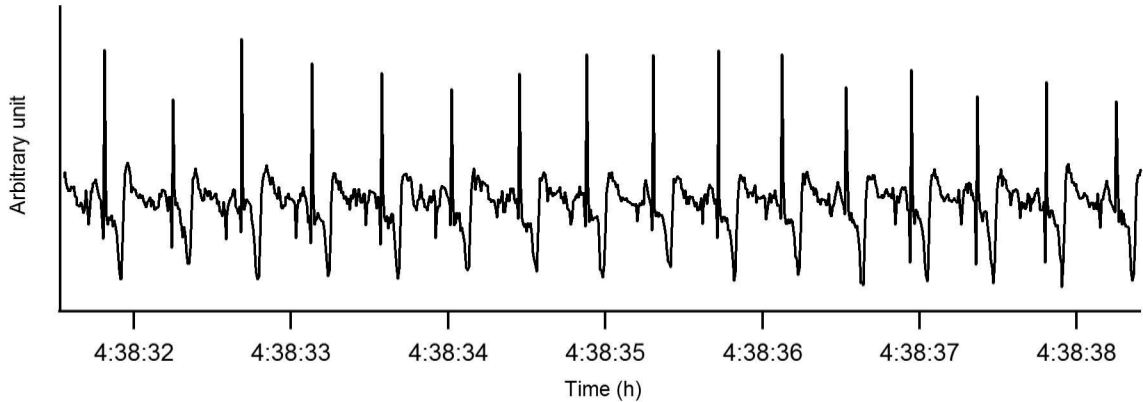
582

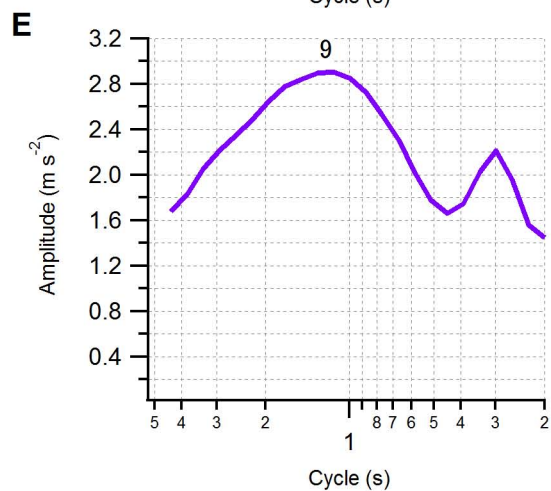
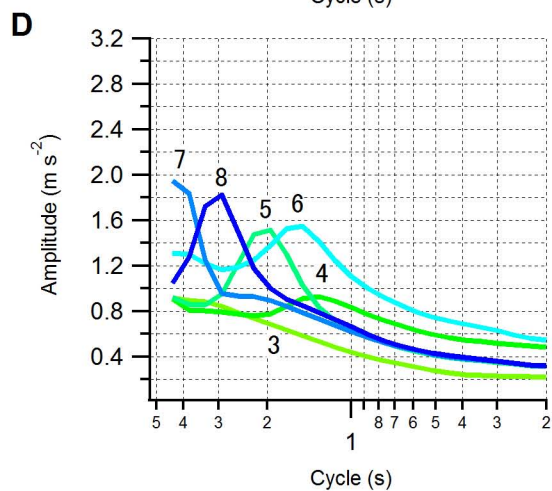
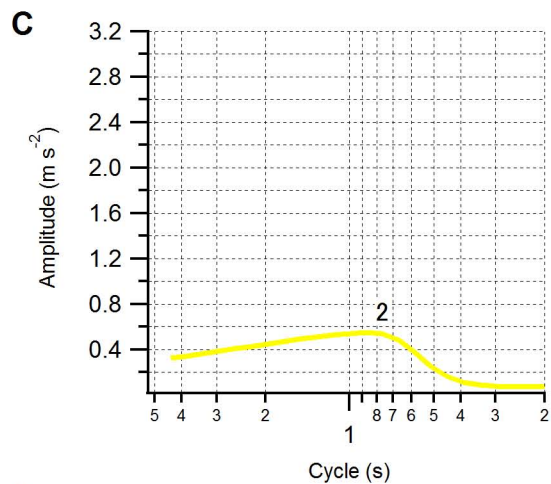
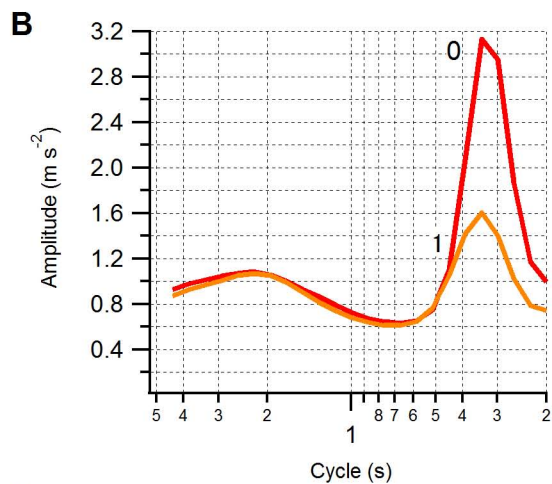
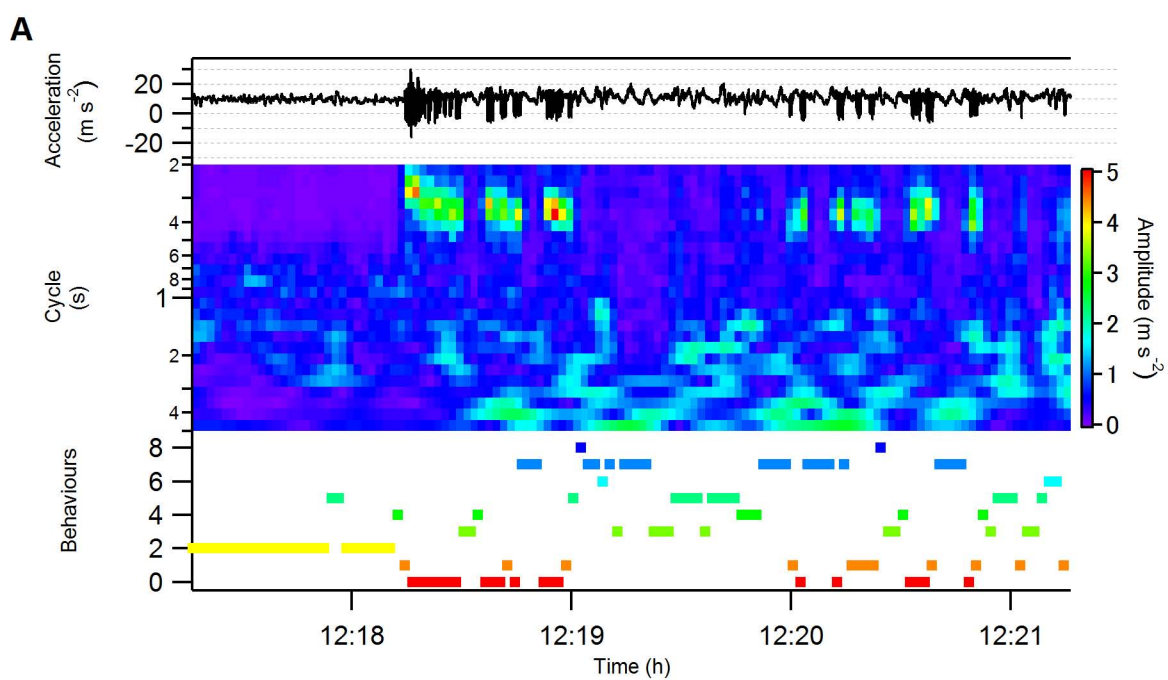
583

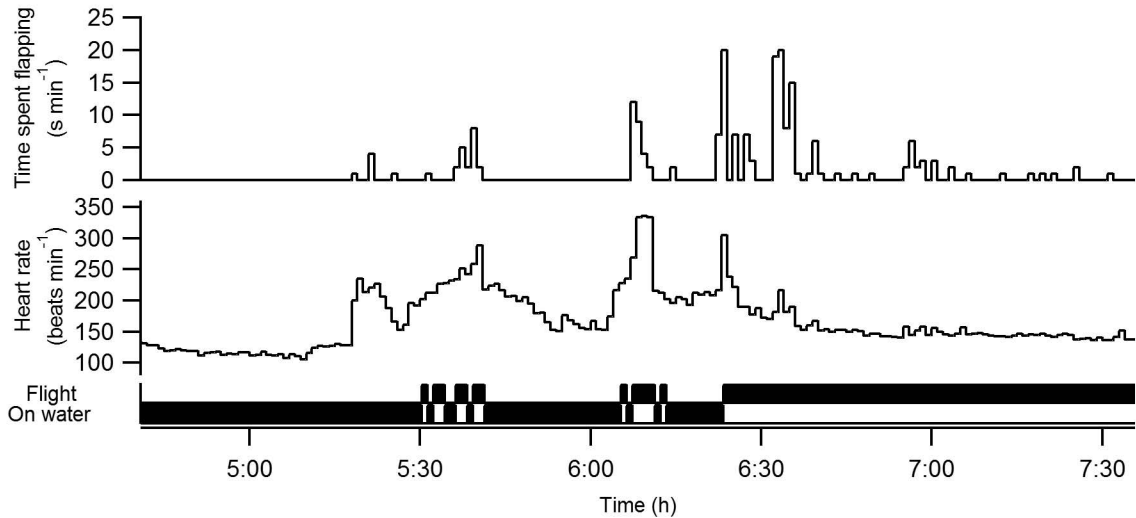
584

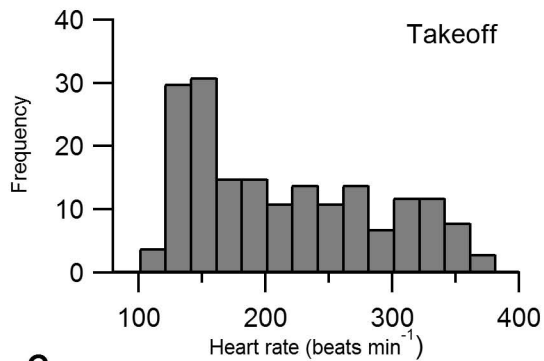
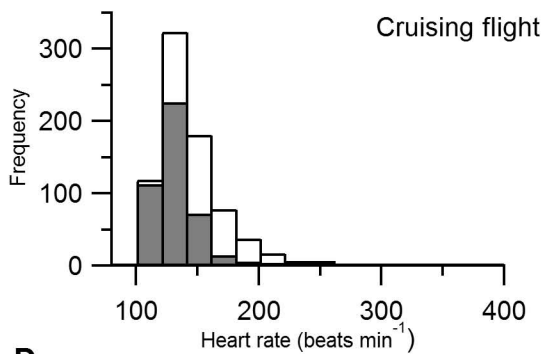
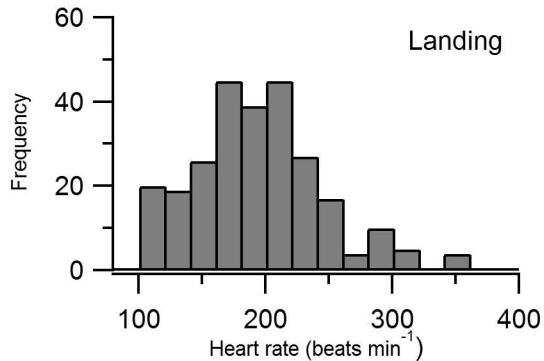
Bird ID	Body mass (kg)	Year	Recorder	Heart rate (beats min ⁻¹)					Time spent in each activity (%)				Time spent flapping (%)		
				Takeoff	Flapping in cruising flight	Gliding in cruising flight	Landing	On water	Takeoff	Cruising flight	Landing	On water	Takeoff	Cruising flight	
BBA1	3.70	2005	Heave & 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

Data are mean ± s.d. Numbers in parentheses indicate recording duration in min.







A**B****C****D**