1   **Title**

2   **Heart rate and estimated energy expenditure of flapping and gliding in**

3   **black-browed albatrosses**

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5   **Short title**

6   Energy cost of flight in albatrosses

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8   **Authors and Affiliations**

9   Kentaro Q. Sakamoto[1]*, Akinori Takahashi[2, 3], Takashi Iwata[2], Takashi Yamamoto[3],

10   Maki Yamamoto[4], Philip N. Trathan[5]

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12   [1]Graduate School of Veterinary Medicine, Hokkaido University, Sapporo 060-0818,

13   Japan, [2]Department of Polar Science, The Graduate University for Advanced Studies,

14   Tachikawa, Tokyo 190-8518, Japan, [3]National Institute of Polar Research, Tachikawa,

15   Tokyo 190-8518, Japan, [4]Department of Bioengineering, Nagaoka University of

16   Technology, Nagaoka 940-2188, Japan, [5]British Antarctic Survey, Natural Environment

17   Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United

18   Kingdom.

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20   * Corresponding author: Kentaro Q. Sakamoto

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

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

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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 expend only 4.6% ± 1.4% of their time in flapping during cruising flight, which was significantly lower than those 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.

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48   **Key words:** black-browed albatross, *Thalassarche melanophrys*, flight, flapping,

49   gliding, heart rate, energy expenditure, accelerometer.

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52 **INTRODUCTION**

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.

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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.

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Instruments

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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).

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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% ± 0.15% (mean ± 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% ± 9.1% of the entire time;

217 mean ± s.d., $n = 8$) or a complete lack of resting behaviour (46.6% ± 11.6% of the entire

218 time; $n = 8$). The combination of both types of behaviour comprised 67.6% ± 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% ± 1.3%; mean

231   ± 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.,

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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.

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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

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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:

$$f_H = 3.278T_f + 131.8 \tag{1},$$

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%, $P < 0.01$).

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301

302   **DISCUSSION**

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

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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

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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% ± 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:

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$$\dot{V}_{O2} = 0.00466 f_H^{1.61} \ (r^2 = 0.79) \tag{2},$$

362   where $\dot{V}_{O2}$ is the rate of oxygen consumption in mL min^{-1} 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 W kg^{-1} × 19.2% + 4.66 W kg^{-1} × 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 ± 0.24 W kg^{-1}; mean ± s.e.m.) and when on the water

376   (5.77 ± 0.41 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 ± 0.17 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.

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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
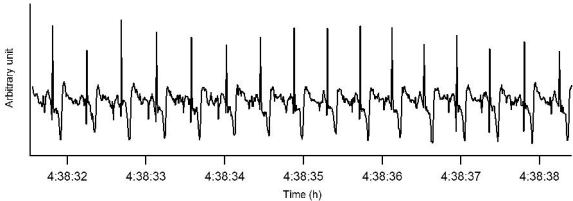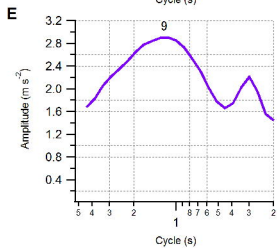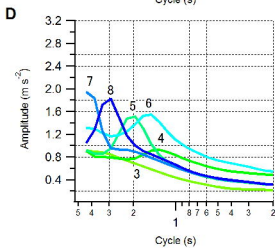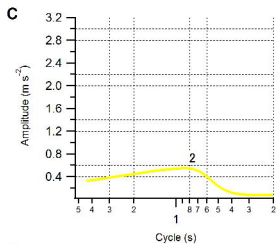
567   different markers ($n = 3$).

568

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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
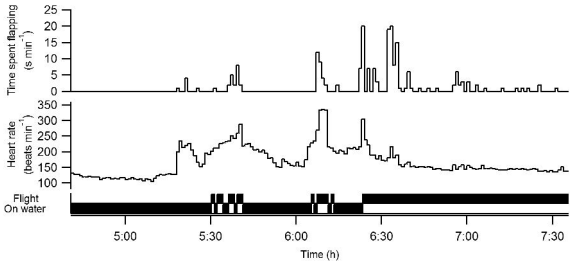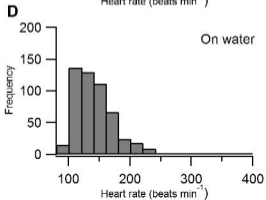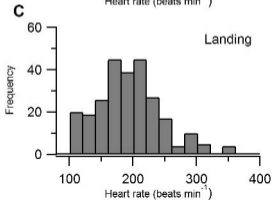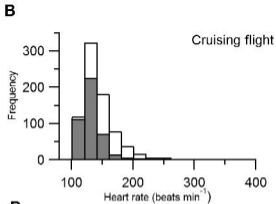
581   when a bird is flying.

582

583

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Axis labels: Arbitrary unit (vertical), Time (h) (horizontal)

Time axis values: 4:38:32, 4:38:33, 4:38:34, 4:38:35, 4:38:36, 4:38:37, 4:38:38

A

B

C

D

E

A Takeoff — Frequency vs Heart rate (beats min⁻¹)

B Cruising flight — Frequency vs Heart rate (beats min⁻¹)

C Landing — Frequency vs Heart rate (beats min⁻¹)

D On water — Frequency vs Heart rate (beats min⁻¹)

A Takeoff

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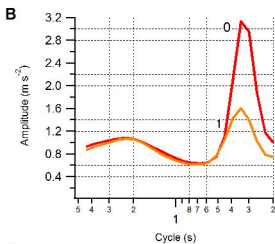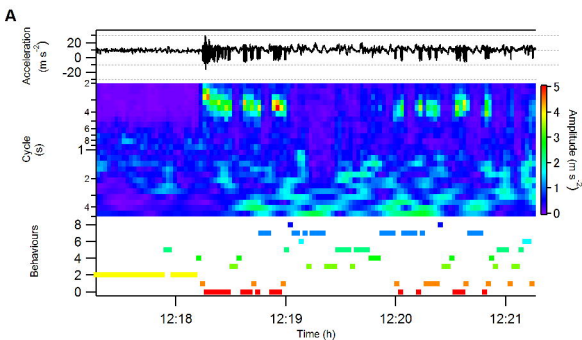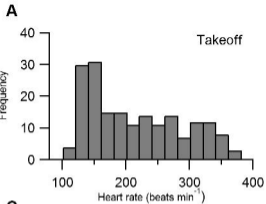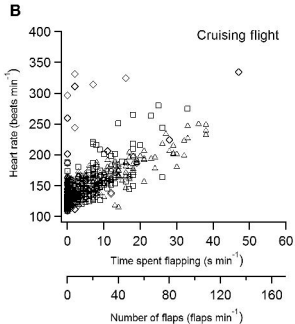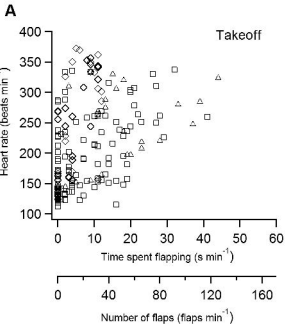
Bird ID	Body mass (kg)	Year	Recorder	Heart rate (beats min^{-1})					Time spent in each activity (%)				Time spent flapping (%)	
				Takeoff	Flapping in cruising flight	Gliding in cruising flight	Landing	On water	Takeoff	Cruising flight	Landing	On water	Takeoff	Cruising flight
BBA1	3.70	2005	Heave &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