



## Supplementary Materials for

### **Frigate birds track atmospheric conditions over months-long transoceanic flights**

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## **Materials and Methods**

### **1. Field study and equipment**

The study was carried out on Europa Island (22.3°S, 40.3°E), in the Mozambique Channel in September-November (period of incubation and small chick brooding) 2011, 2012 and 2013 and in January-March (period of large chick rearing and fledging) 2014 and 2015. Adults brooding small chicks or feeding large chicks, and juvenile birds were captured on or nearby the nests using a long telescopic pole equipped with a noose by day, or by hand using night vision goggles at night. In addition, direct observations of flight of frigatebirds over land and at sea were made from Europa.

To study large scale migratory movements, 24 adults and 25 juvenile birds were equipped with PTT 100 (Microwave Telemetry, Columbia, USA) 9.5 g solar powered Argos Transmitters and 20 g Solar GPS/PTTs (6 juveniles). To study the relationship between heart rate, activity (flapping frequency) and behaviour (ascent rates, horizontal speed), 11 adult females were equipped with an external 18 g custom designed loggers measuring tri-axial acceleration and electrocardiography (25) and a GPS (i-gotU GT-120, Mobile Action Technology Inc., Taipei, Taiwan, 18 g). Birds were recaptured and the loggers recovered after one or several foraging trips at sea. To study movements and activity, 37 adult females and males were equipped with Solar powered GPS-Accelerometers (GPS-RF, e-obs GmbH, Munich, Germany, 22g), whose data are recovered regularly by an automatic recording station installed in the colony. In addition the loggers measured external temperature. All loggers were attached to feathers on the back of birds with adhesive tape, centred between the wings to allow optimal accelerometer measurements. For long term deployments, loggers detached from the birds during moulting after variable durations of transmissions (range 3-25 months). The total mass of logger(s) was always below 3% of the bird body mass for short term deployments and below 1% of bird body mass for long term deployments (> 2 months). The field procedures and manipulations on Europa were given permission by the 'Préfet of Terres Australes et Antarctiques Françaises'.

### **2. Analyses:**

#### **2.1. Heart rate and accelerometry loggers**

The data loggers recorded tri-axial acceleration (100 Hz) and ECG (180Hz). ECG data was post-processed to obtain heart rate ( $f_h$ , beats  $\text{min}^{-1}$ ) using a custom QRS-complex detection algorithm. Data processing and analysis of ECG follow (5). The three acceleration axes collected at 100 Hz were first individually calibrated using static data collected on all azimuths while the tags were still on a hard surface. Dynamic Body Acceleration (DBA) was calculated from the method in (26). In short, the calibrated signal was first filtered using a 3<sup>rd</sup> order low-pass filter with a cut-off frequency at 12 Hz (Matlab *ifilter* function). We then calculated the tri-axial static acceleration (i.e., a vector aligned with the dorso-ventral axis) and scalar projected the raw acceleration onto the vertically aligned tri-axial static acceleration to obtain the vertically aligned acceleration. The vertically aligned acceleration was thus filtered with a high-pass filter with a cut-off frequency at 2 Hz to extract the vertical dynamic acceleration. DBA was obtained by calculating the root mean square (RMS) of the vertically aligned dynamic acceleration over periods of 1 s.

The wing beat events were detected using the zero-crossing method detailed in (27) applied on the dynamic vertical acceleration (which is centered around  $0 \text{ ms}^{-2}$ ). In short, we calculated the RMS value between 2 successive zero-crossings and considered a flapping event when RMS values were above  $2 \text{ m/s}^2$ . The relative body power induced by a wing beat event was calculated by squaring its RMS value and dividing it by its frequency (i.e. by the reciprocal of the period of time elapsed between the beginning and the end of the wing beat or between the 2 zero-crossings of the event) and further division by two times Pi squared (2). The flapping frequency while flying was measured by counting the number of detected wingbeats per second of flight.

## 2.2 Flight tracks and flight behaviors

Altitudes were obtained from the GPS logger recording at interval of 2 sec to 2 min according to deployment, with a precision of  $\pm 5\text{m}$ . Since frigatebirds fly at altitude and come to the sea surface to feed, we separated the tracks into Active Foraging phases when birds came at altitude under 30m, and Travelling phases when birds were at altitude higher than 30 m based on previous studies and observations (9). We separated the flight between 2 GPS locations (every 1-5 min) into 6 behaviors related to vertical movements, Gliding, Active Descent with frequent flapping, Soaring, Active Ascent with frequent flapping, Constant altitude with or without flapping (see Table S1) using the combination of altimetry and accelerometry.

Argos data were filtered using a speed filter set at maximum speed of 70 km/h (9). We used civil twilight measured from ephemerides at the location obtained from the GPS or Argos transmitter to separate night and day time.

### 2.3. Environmental data

Standard wind UGRD (i.e. East-West component in m/s), VGRD (North-South component in m/s), wind magnitude (or speed m/s) and azimuths (direction in degrees from North) archived data were downloaded from the National Oceanic and Atmospheric Administration's Operational Model Archive and Distribution System (NOAA-NOMADS) using the rNOMADS package in R (author D.C. Bowman, in R 3.2.1). Four daily wind metrics were extracted at time, latitude, longitude and altitude of each bird closest to one of the measured points in the archived database. Consequently, the times at which GPS locations were taken were binned to the closest of one of the 4 time slots, the locations of the birds at these specific times were clustered within a latitude and longitude grid and the altitude of the bird to the closest archived altitude. Altitudes that were measured below 0 m were corrected and considered to be at the surface. Climatologies of wind direction and wind speed were obtained from the Earth System Research Laboratory (NOAA) website: <http://www.esrl.noaa.gov/psd/data/histdata/>

### 2.4. Cumulus clouds

No information was available to us on the presence of cumulus clouds on the tracks. On figures 2 or 4 of the presence of clouds was derived from the behaviour of birds. An ascending flight without or with little flapping of wings can only be made with support of an ascending air current. At sea an ascending air current can only exist in a thermal below a cumulus cloud. In an area not below a cumulus cloud, there is no rising air. In this area the air is moving only horizontally or moving downward in terms of a downdraft. Thus, it can be concluded that there is a cumulus cloud where the bird performs an ascending flight, when birds climb without flapping their wings. Soaring outside but close to the clouds would not be possible because of the downdrafts occurring in the near vicinity of cloud-edges (Fig. 4).

### 2.5. Statistics

Statistical analyses were made using Statistica 12. All values are given as mean  $\pm$  one S.D. unless stated otherwise.

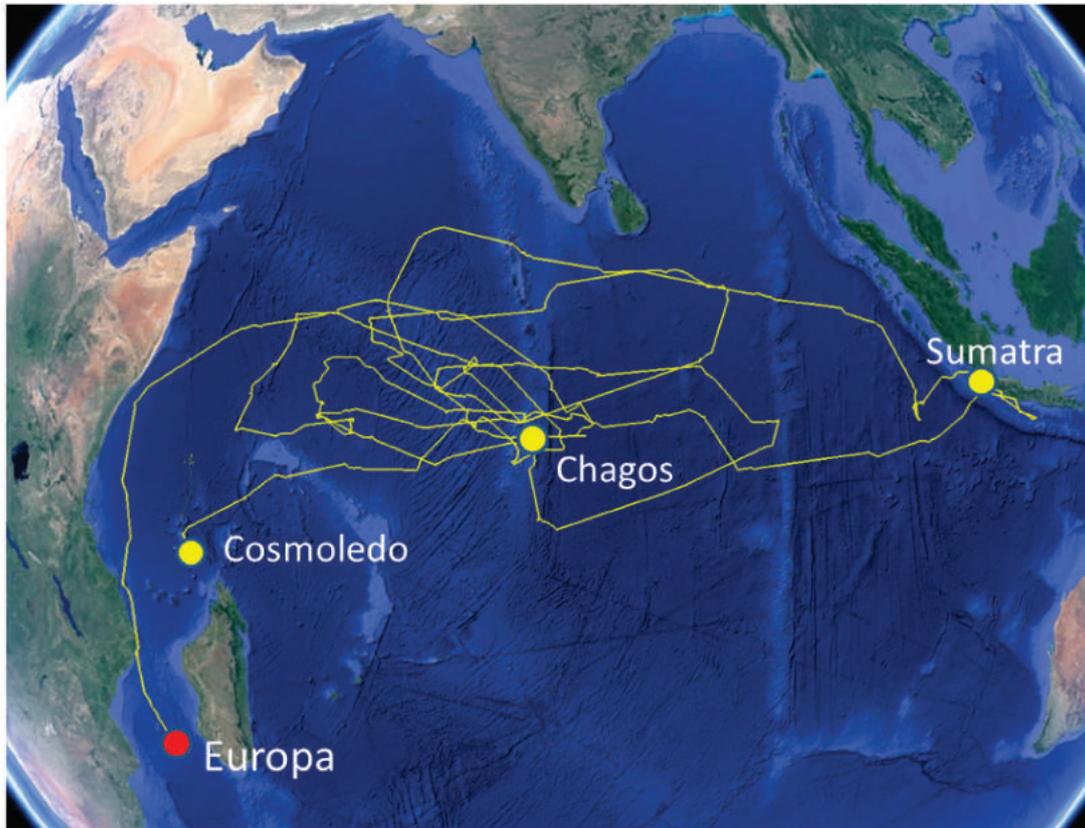
## Supplementary text

### Estimated calibration curve for frigatebird heart rate measurements.

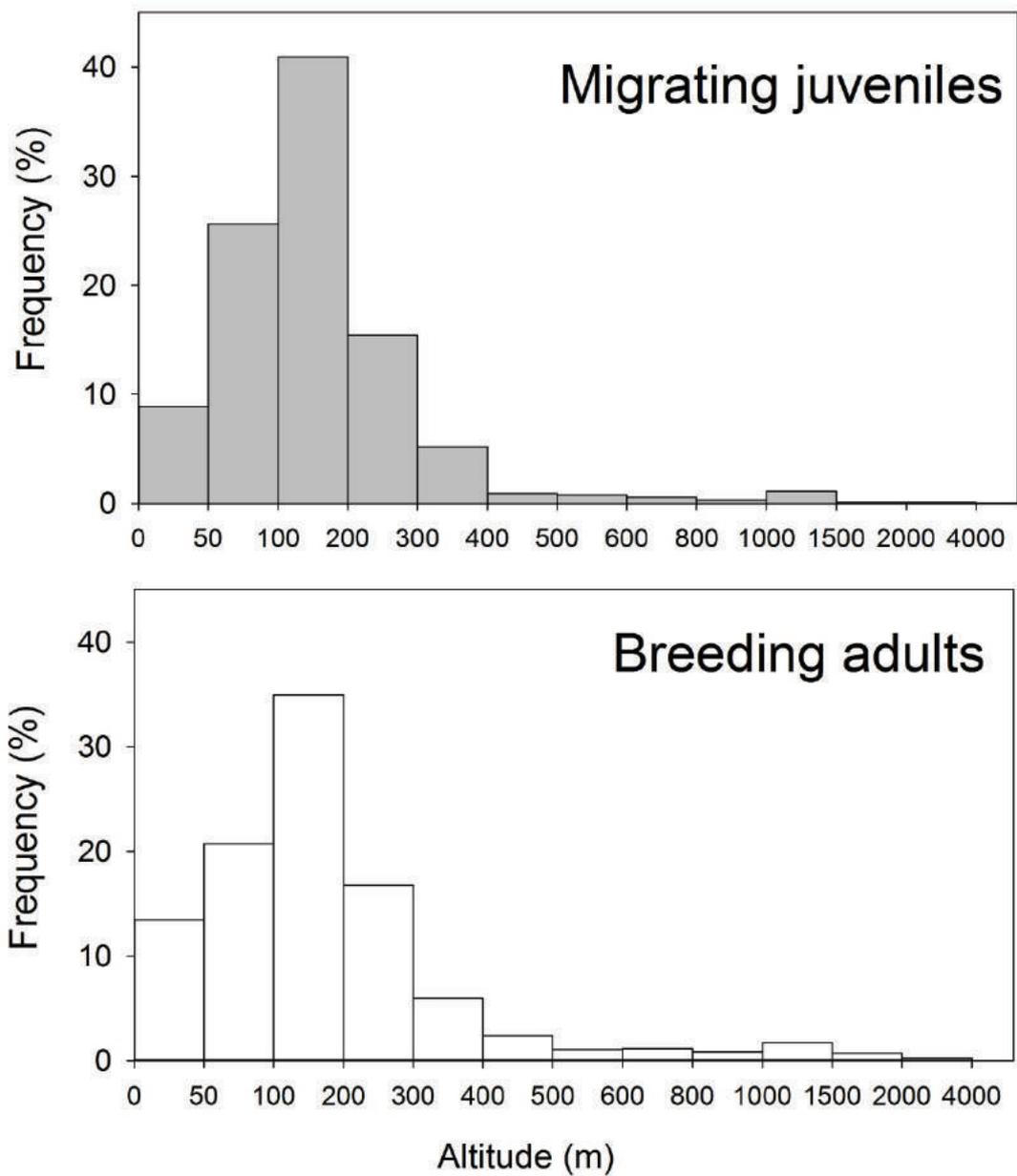
Root mean square (DBA) and estimates of body power ( $P_b$ ) are uncalibrated and so provide relative estimates of effort. Heart rate was not measured on most birds, so DBA is the most useful variable for investigating relative energy expenditure and relative flight performance across a larger group of birds. However, it has been shown that for endothermic vertebrates exercising using their primary mode of locomotion there is a general allometric relationship between heart rate and rates of oxygen consumption, when normalizing for body and heart mass (28). Thus, for birds of a similar body and heart mass, it might be expected that there will be a generally similar relationship between heart rate and energy consumption. The only species of birds for which there is a calibration during flight are for the barnacle and bar-headed geese (29), with mean body mass of 2 and 2.8 kg, respectively. The frigatebirds in this study are only slightly smaller, at a range of 1.2 to 1.42 kg, while the relative heart size of two magnificent frigatebirds was 0.81 and 1.03% of body mass (30), which is almost identical to that of the geese. Using the calibration data from the geese (Fig. S5) we can plot estimates for values representing basal metabolic rate (BMR), field metabolic rate (FMR) and maximum aerobic metabolic rate (MMR) based on our data and those from the literature, while normalizing for both body and heart mass (28). Resting heart rate in the present study averaged 71.2 beats  $\text{min}^{-1}$  and Enger (31) used indirect calorimetry to measure BMR in *Fregata magnificens* ranging between 50 to 70  $\text{kcal day}^{-1}$  (or 6.64  $\text{ml min}^{-1} \text{kg}^{-1}$ ). Overall average heart rate while airborne in the present study averaged 203 beats  $\text{min}^{-1}$ . Dearborn et al. (32) used doubly-labelled water to measure the FMR in *Fregata minor*, average 677  $\text{kJ day}^{-1}$  (or 17.93  $\text{ml min}^{-1} \text{kg}^{-1}$ ), but this was during 2 days of the breeding season when birds were mostly displaying at their leks. More realistically, Ellis and Gabrielsen (33) calculated an allometric relationship for the FMR of 37 species of seabird that gives a prediction for a 1.3 kg frigatebird of 1268  $\text{kJ day}^{-1}$  (33.6  $\text{ml min}^{-1} \text{kg}^{-1}$ ). Finally, we can use the heart mass ( $M_h$ ) of the frigatebird to predict the maximum theoretical rate of oxygen consumption of a frigatebird with a relative heart mass of 0.92% of body mass, using the relationship  $33M_h^{0.88}$

which gives reasonably accurate values when used to predict maximum performance in geese (34)(Figs. S5, S6). Maximum heart rates detected in the present study are between 500 and 550 beats  $\text{min}^{-1}$ , on a few occasions. This comparative analysis suggests that using the calibration data from geese and normalizing for differences in body and heart mass is likely to give approximate but realistic values for the field energetics of the frigatebirds. The results are broadly in agreement with the allometric analysis (33). However, it should be emphasized that, unlike most of the other species of seabird, frigatebirds are continuously airborne. Thus, it indicates that the FMR for these birds during months at sea is likely to be exceptionally low and comparable to that of walking in terrestrial birds such as geese (or between 2.5 and 5 times BMR).

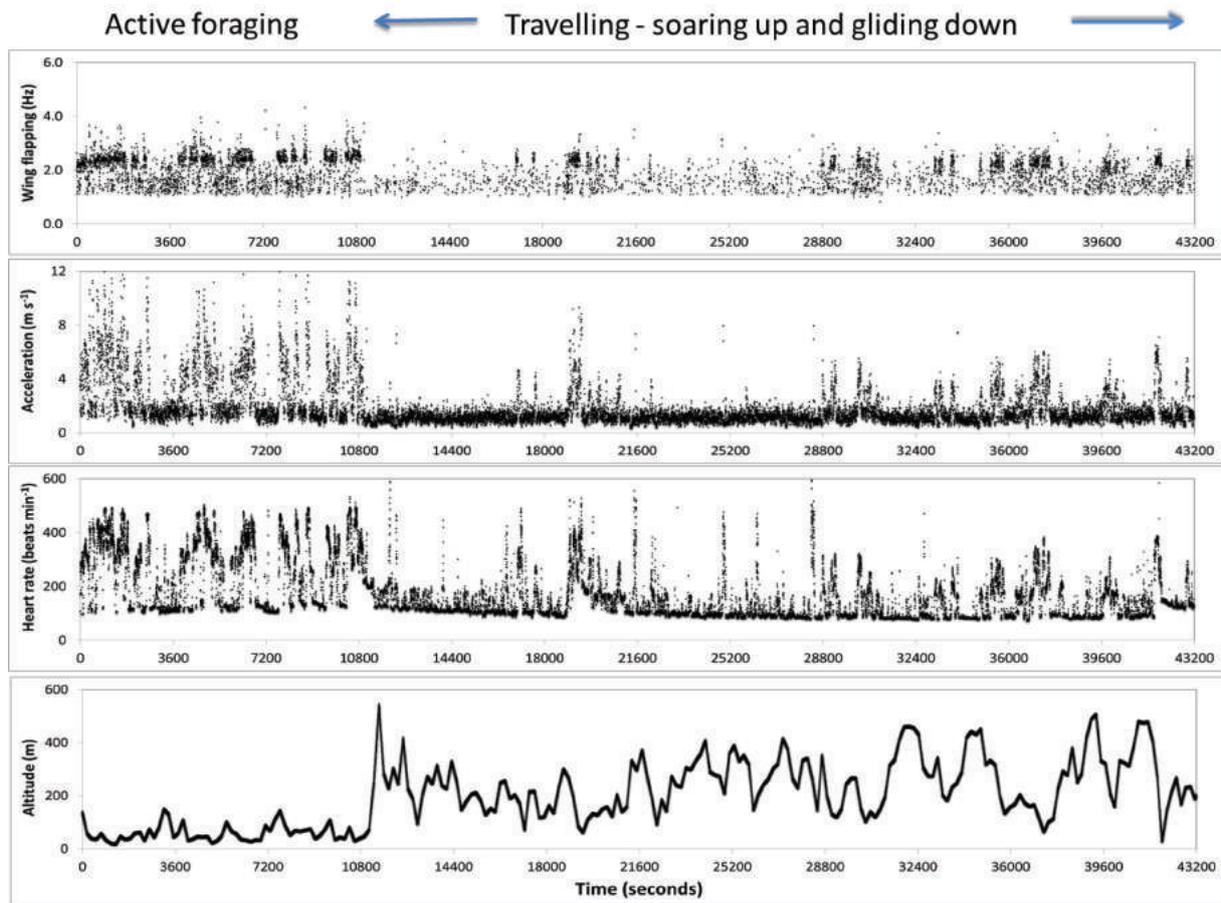
## Supplementary figures



**Fig. S1.** Six months track of juvenile 130474 fledged from Europa and moving over the entire Indian Ocean covering 55.743 km. The young bird landed very briefly on an islet off Sumatra, and on several islets of the Chagos for a total of 3.7 days over the 185 tracking period. The Argos transmitter stopped emitting briefly after a short stop on Cosmoledo Island,

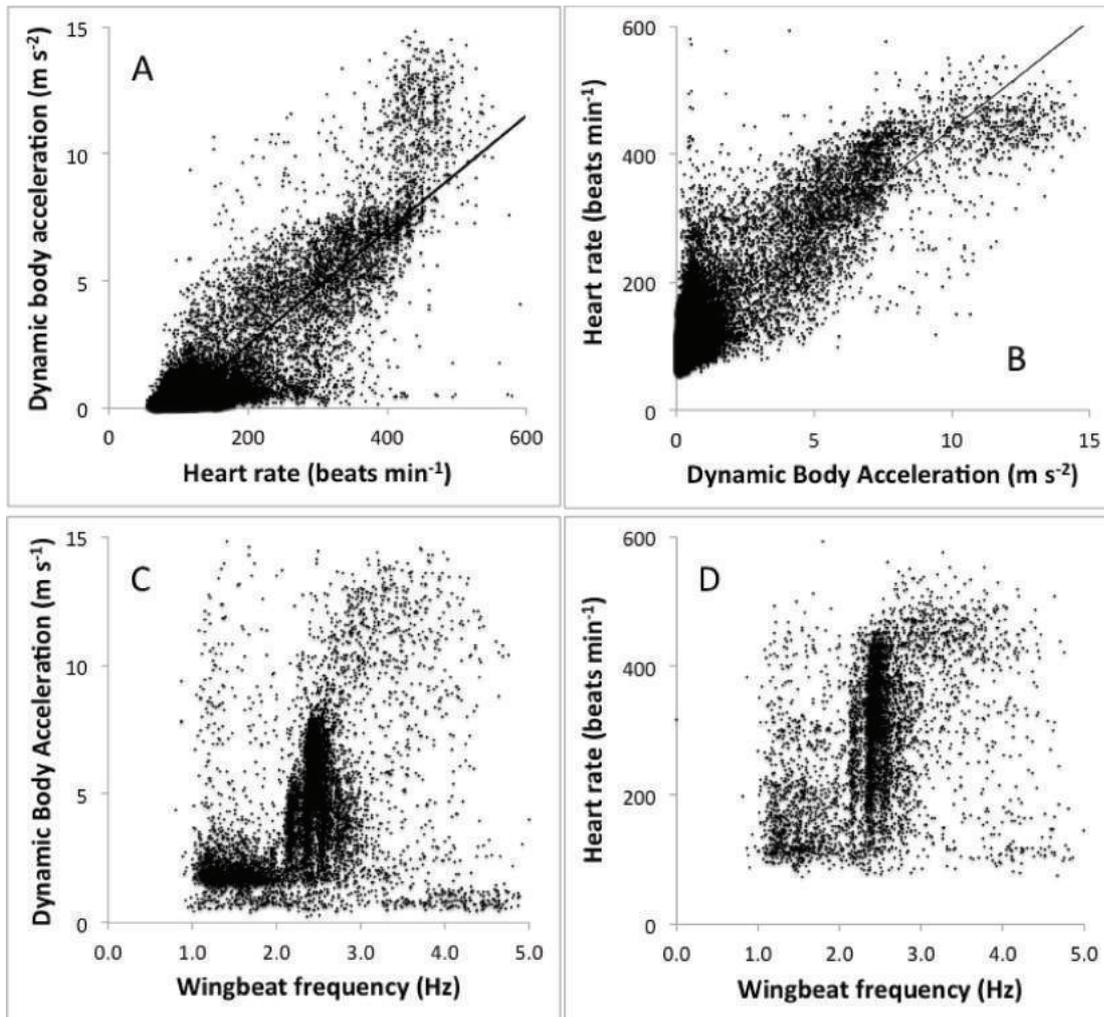


**Fig. S2.** Frequencies of altitudes used during transoceanic flights of juveniles and during breeding by great frigatebirds

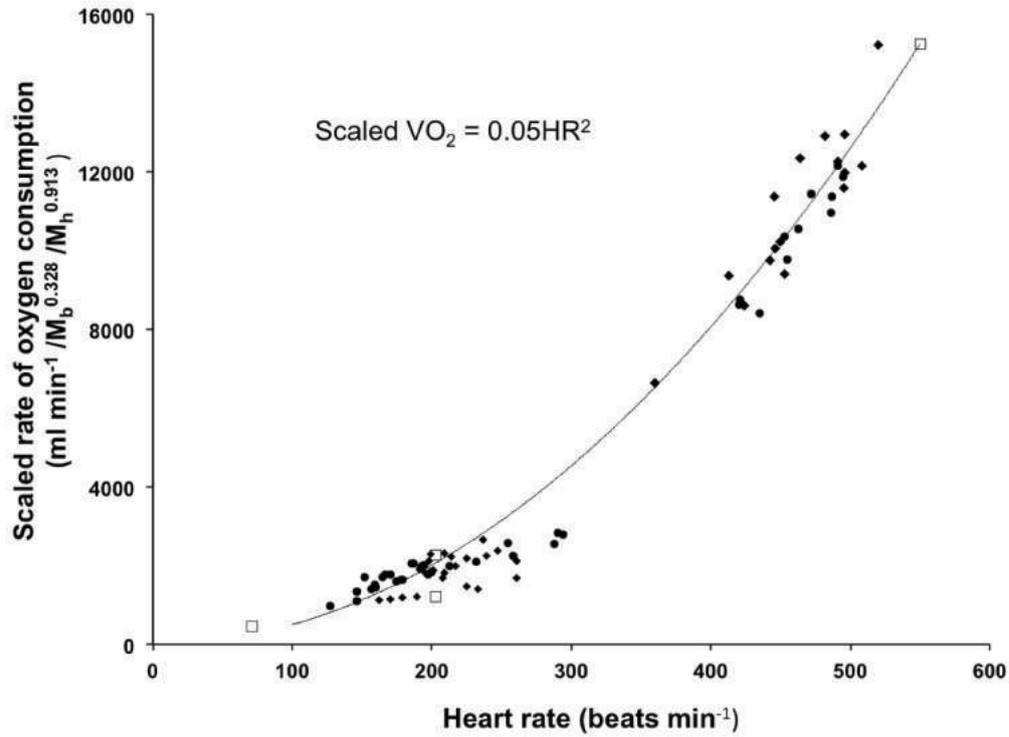


**Fig. S3.** Changes in altitude, heart rate and flight parameters of frigatebirds.

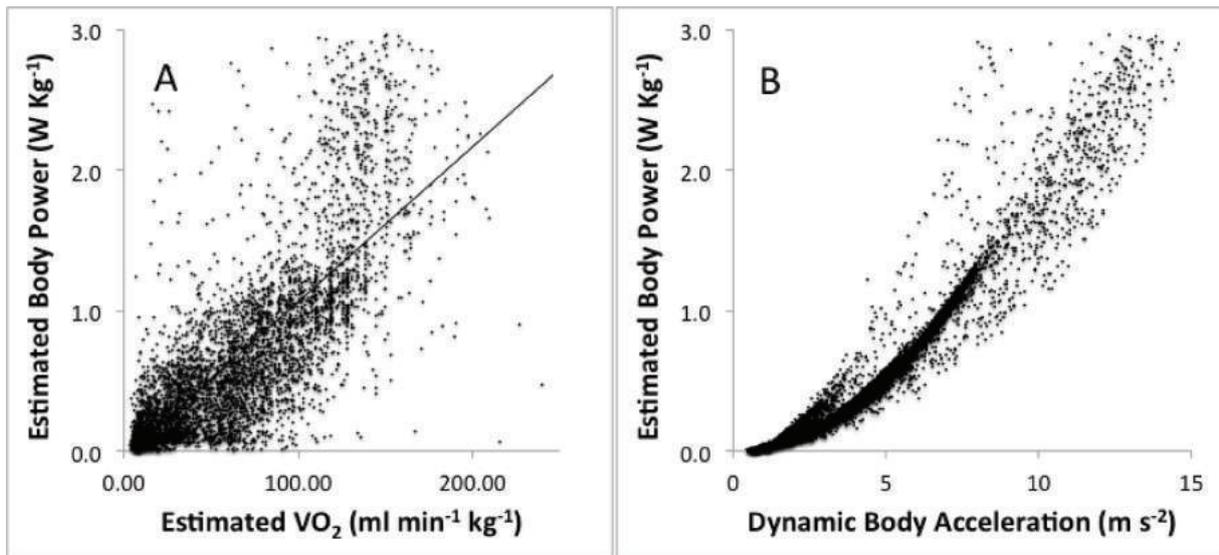
Wingbeat frequency, dynamic body acceleration (DBA), heart rate and altitude of a great frigatebird during a 12 foraging trip from Europa Island. For the first 3 hours the bird spent most of its time low over the water and actively foraging, indicated by intense bouts heart rates above 400 beats  $\text{min}^{-1}$ , associated with DBA values about 6  $\text{m s}^{-1}$  and consistent flapping around 2.5 Hz. The next 9 hours are spent routinely soaring up to between 300 to 600 m, followed by gradual gliding descents. Heart rates and values of DBA and wingbeat frequency are generally very low during the ascending flights, with frequent periods with no wing beat.



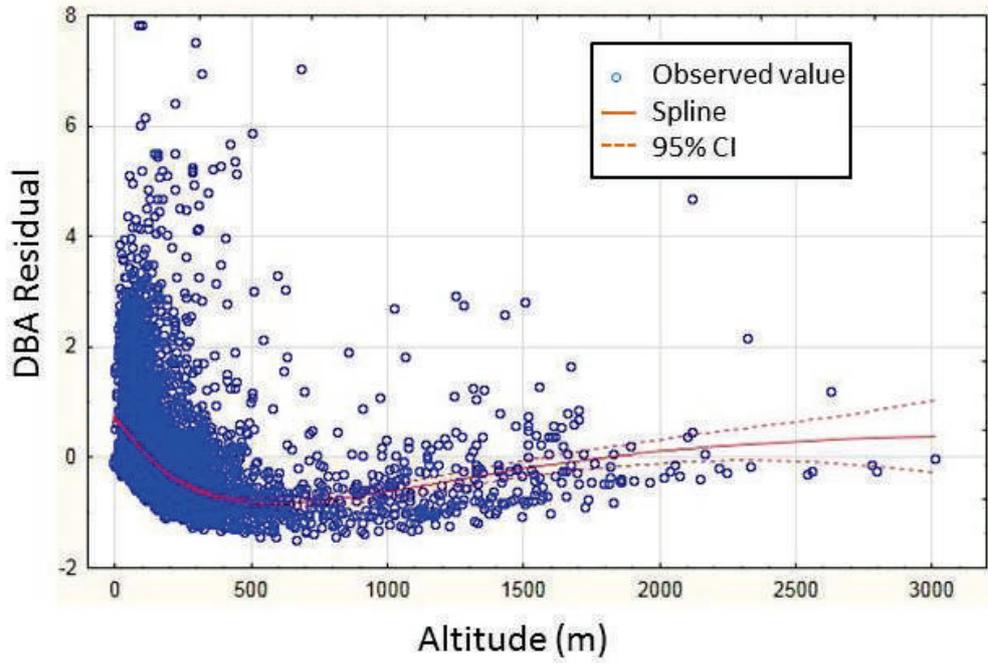
**Fig. S4.** Data collected from a single frigatebird over 72 hours of flight. **(A)** Root mean square dynamic body acceleration (DBA) against heart rate (HR), linear regression was fitted to the raw data as  $DBA = 0.023HR - 2$ ,  $R^2 = 0.76$ , **(B)** heart rate plotted against DBA, linear regression  $HR = 33.8DBA + 101$ ,  $R^2 = 0.76$ . **(C)** and **(D)** show DBA and heart rate plotted against wingbeat frequency, respectively. They show that wingbeat frequency was predominantly centered around 2.5 Hz with a variance of less than 0.5 Hz, and that it was largely independent of proxies for either mechanical power (DBA) or Estimated body power (not shown) or metabolic power (heart rate). Thus, power was primarily modulated by numbers of flaps in a bout or by wingbeat amplitude. Values of wingbeat frequency above 3 flaps  $s^{-1}$  are generally linked to DBA values  $>9 m s^{-2}$  and appear to be associated with heart rates of less than 550 beats  $min^{-1}$ . These may represent brief but powerful wingbeats where the cardiovascular response is too slow to reflect the effort involved and where the muscle is effectively working anaerobically.



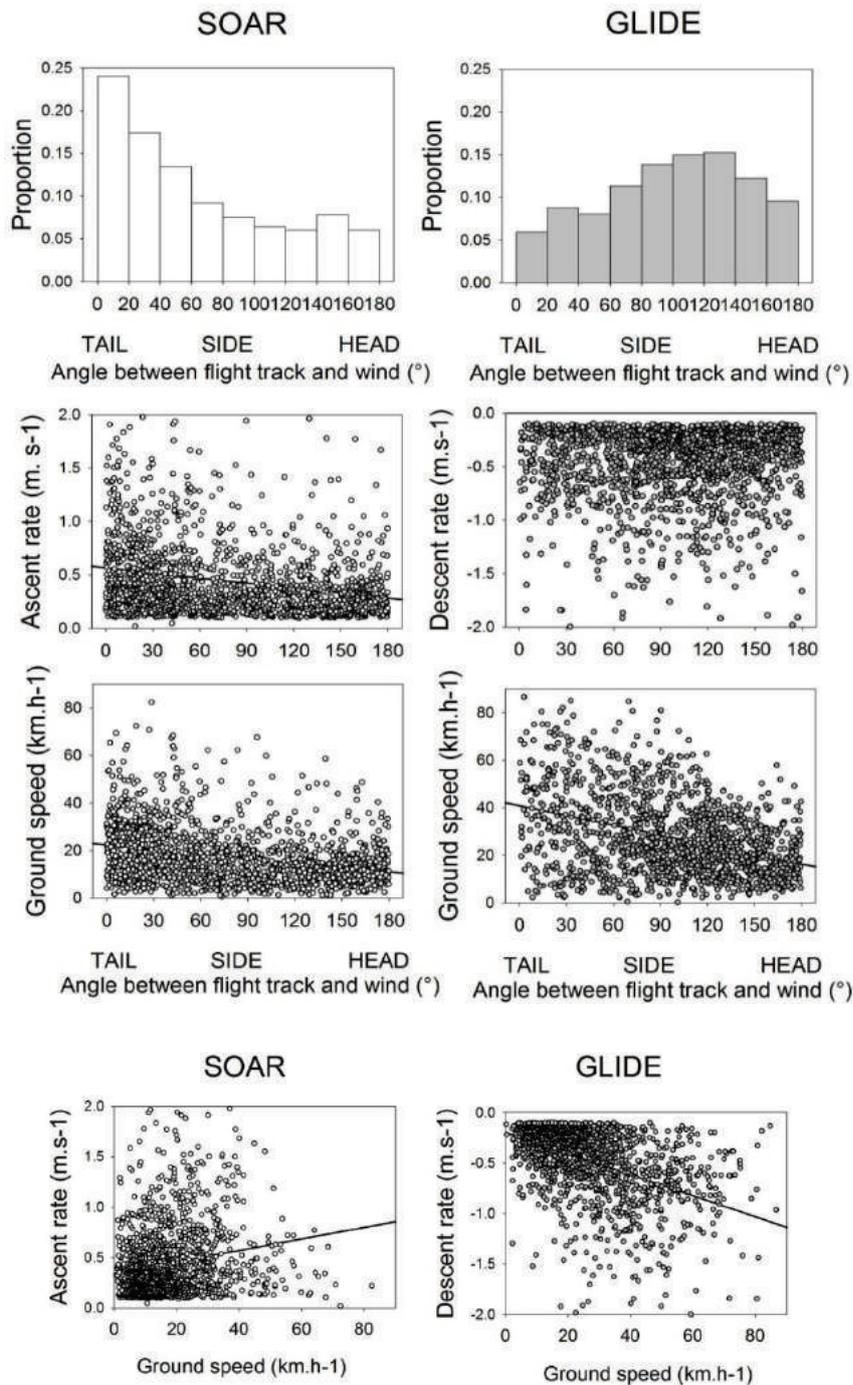
**Fig. S5.** Estimated calibration curve for a frigatebird based on (28), with data taken from (29) and papers named in above text. The power curve is extrapolated backwards from the estimated maximum metabolic rate point with heart rate at 550 beats per minute and assuming an exponent of 2 (i.e. that scaled rate of oxygen consumption is proportional to heart rate squared).



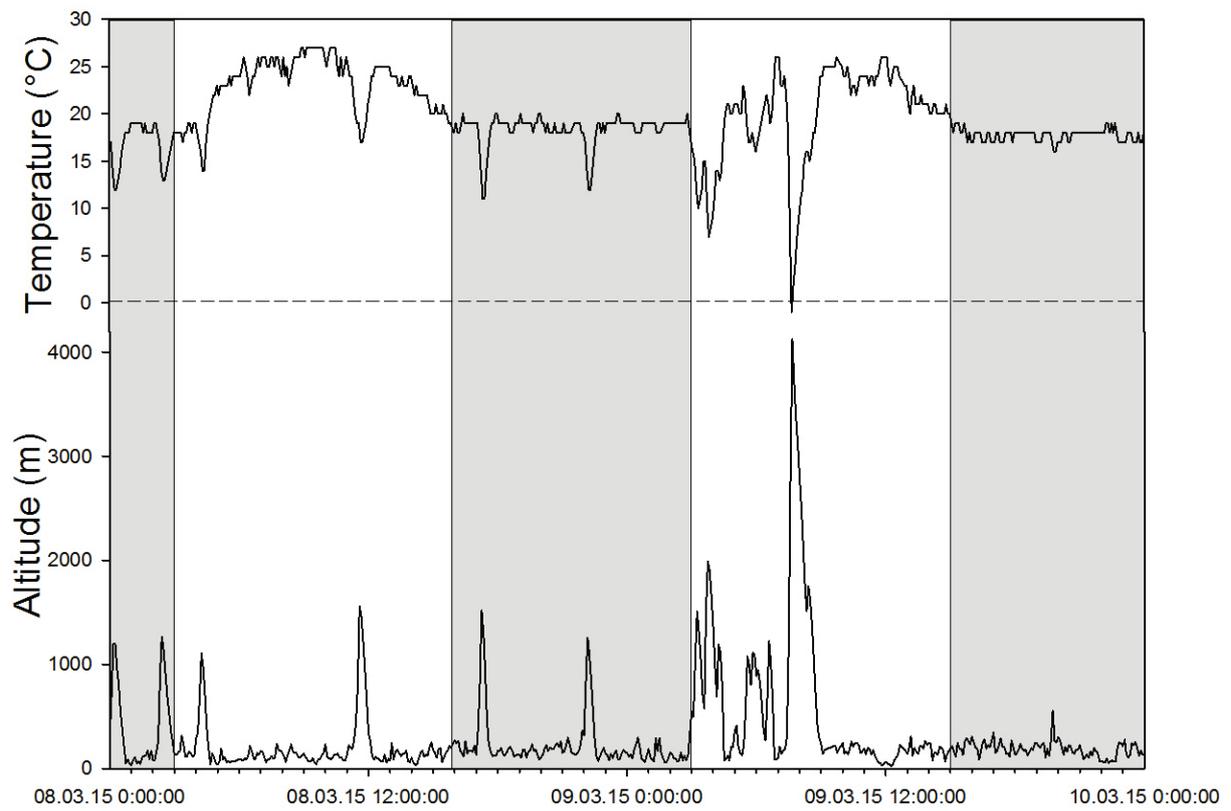
**Fig. S6.** Estimated body power (W kg<sup>-1</sup>) plotted against (A) estimated rate of oxygen consumption (VO<sub>2</sub>, ml min<sup>-1</sup> kg<sup>-1</sup>) with linear regression  $y = 0.11X - 0.041$ ,  $R^2 = 0.585$  and (B) dynamic body acceleration (m s<sup>-2</sup>).



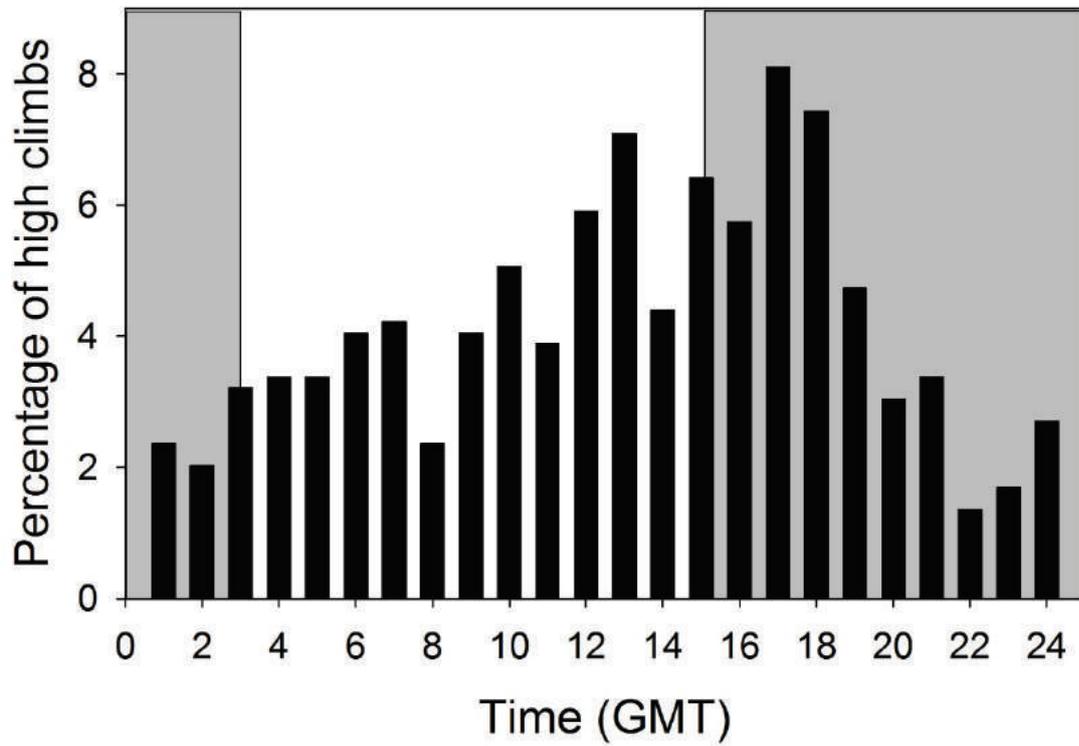
**Fig. S7.** Response curve of Dynamic Body Acceleration DBA to altitude when travelling (General Additive Model, pseudo R2 = 0.23, Poisson distribution)



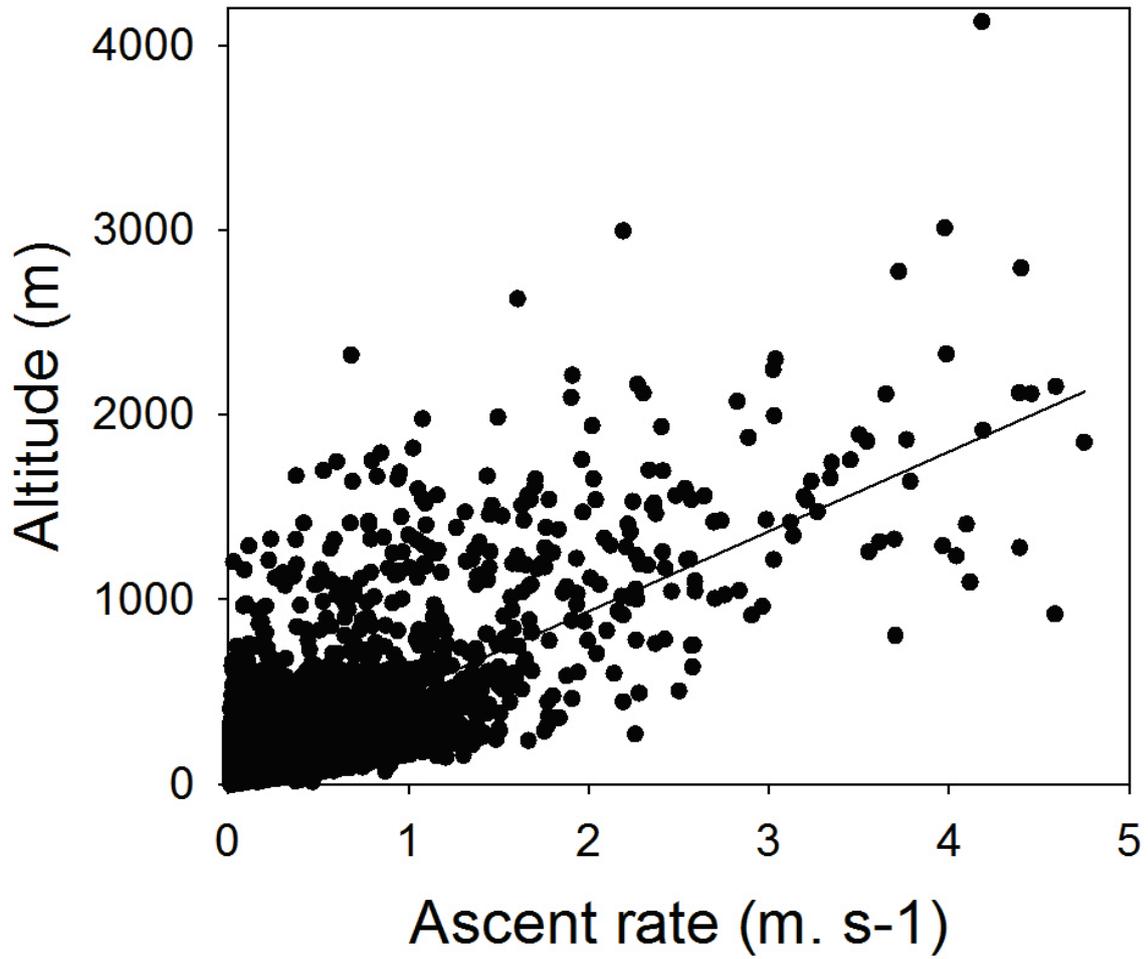
**Fig. S8.** Proportion of flight tracks between 2 locations during soaring and gliding when flying with tail to head winds (Top graphs). Middle and lower figures: ascent rate and ground speed in relation to the angle between flight track and wind direction when soaring and gliding. Relationship between ascent rate (m/s) and ground speed (km/h) when soaring and gliding. Data for 8 different individuals pooled.



**Fig. S9.** Temperature and altitude recorded during a 3-day foraging movement of an adult female, showing a drop in ambient temperature below 0°C during a climb to 4000m.



**Fig. S10.** Distribution of high climbs (higher than 700m) throughout the day, showing an increase in the frequency of high climbs peaking at dusk and during the first hours of darkness (n=263 foraging trips of 15 adult birds). Shaded grey areas represent night-time.



**Fig. S11.** Relationship between altitude and climb rate ( $y = 432x + 72$ ,  $R^2 = 0.539$ ,  $P < 0.001$ , for 8 individuals pooled), Climb rates were on average  $0.41 \pm 0.29 \text{ m s}^{-1}$  below 600 m, and  $1.86 \pm 1.13 \text{ m s}^{-1}$  above 600 m ( $F_{1,7} = 21.2$ ,  $P = 0.006$ ).

**Table S1-** The six behaviors attributed to vertical movements of great frigatebirds

abbreviation	Behavior	Flapping frequency	Ascent rate criteria	Mean Ascent rate (m/s)
NO	No ascent or descent steady flight	<10 beat/min	+/- 0.1 m/s	
FLAP	Flapping during steady flight	>10 beat/min	+/- 0.1 m/s	
SOAR	Soaring	<10 beat/min	>0.1 m/s	0.46±0.42
AA	Active ascent	>10 beat/min	>0.1m/s	0.35±0.5
GLID	Gliding	<10 beat/min	<-0.1m/s	-0.49±0.44
AD	Active descent	>10 beat/min	<-0.1m/s	-0.41±0.38

## REFERENCES AND NOTES

1. G.-R. Walther, E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, F. Bairlein, Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002). [Medline doi:10.1038/416389a](#)
2. B. Kranstauber, R. Weinzierl, M. Wikelski, K. Safi, Global aerial flyways allow efficient travelling. *Ecol. Lett.* **18**, 1338–1345 (2015). [Medline doi:10.1111/ele.12528](#)
3. T. Alerstam, Å. Lindström, Optimal bird migration: The relative importance of time, energy, and safety, in *Bird Migration: Physiology and Ecophysiology*, E. Gwinner, Ed. (Springer, 1990), pp. 331–351.
4. J. Rayner, The mechanics of flight and bird migration performance, in *Bird Migration: Physiology and Ecophysiology*, E. Gwinner, Ed. (Springer, 1990), pp. 283–299.
5. C. M. Bishop, R. J. Spivey, L. A. Hawkes, N. Batbayar, B. Chua, P. B. Frappell, W. K. Milsom, T. Natsagdorj, S. H. Newman, G. R. Scott, J. Y. Takekawa, M. Wikelski, P. J. Butler, The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science* **347**, 250–254 (2015). [Medline doi:10.1126/science.1258732](#)
6. R. E. Gill, T. L. Tibbitts, D. C. Douglas, C. M. Handel, D. M. Mulcahy, J. C. Gottschalck, N. Warnock, B. J. McCaffery, P. F. Battley, T. Piersma, Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? *Proc. Biol. Sci.* **276**, 447–457 (2009). [Medline](#)
7. M. H. Dickinson, C. T. Farley, R. J. Full, M. A. Koehl, R. Kram, S. Lehman, How animals move: An integrative view. *Science* **288**, 100–106 (2000). [Medline doi:10.1126/science.288.5463.100](#)
8. C. Pennycuick, *Bird Flight Performance: A Practical Calculation Manual* (Oxford Univ. Press, Oxford, 1989).
9. H. Weimerskirch, M. Le Corre, S. Jaquemet, M. Potier, F. Marsac, Foraging strategy of a top predator in tropical waters: Great frigatebirds in the Mozambique Channel. *Mar. Ecol. Prog. Ser.* **275**, 297–308 (2004). [doi:10.3354/meps275297](#)
10. J. B. Nelson, The breeding biology of frigatebirds - a comparative review. *The Living Bird* **14**, 113–155 (1976).
11. C. J. Pennycuick, Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis* and *Coragyps atratus*. *J. Exp. Biol.* **102**, 307–325 (1983).
12. H. Weimerskirch, O. Chastel, C. Barbraud, O. Tostain, Flight performance: Frigatebirds ride high on thermals. *Nature* **421**, 333–334 (2003). [Medline doi:10.1038/421333a](#)
13. See the supplementary materials on Science Online.
14. A. Laing, J. M. Evans, *Introduction to Tropical Meteorology: A Comprehensive Online & Print Textbook*, Comet Program, A. Laing, Ed. (University Corporation for Atmospheric Research, Boulder, CO, 2011).
15. J. S. Malkus, Some results of a trade-cumulus cloud investigation. *J. Meteorol.* **11**, 220–237 (1954). [doi:10.1175/1520-0469\(1954\)011<0220:SROATC>2.0.CO;2](#)

16. U. Nair, R. Weger, K. Kuo, R. Welch, Clustering, randomness, and regularity in cloud fields: 5. The nature of regular cumulus cloud fields. *J. Geophys. Res. Atmos.* **103**, 11363–11380 (1998).
17. C. J. Pennycuick, *Modelling the Flying Bird* (Elsevier, 2008).
18. T. Alerstam, D. Christie, A. Ulfstrand, *Bird Migration* (Cambridge Univ. Press, 1993).
19. F. Liechti, W. Witvliet, R. Weber, E. Bächler, First evidence of a 200-day non-stop flight in a bird. *Nat. Commun.* **4**, 2554 (2013). [Medline doi:10.1038/ncomms3554](#)
20. N. C. Rattenborg, Do birds sleep in flight? *Naturwissenschaften* **93**, 413–425 (2006). [Medline doi:10.1007/s00114-006-0120-3](#)
21. J. A. Lesku, N. C. Rattenborg, M. Valcu, A. L. Vyssotski, S. Kuhn, F. Kuemmeth, W. Heidrich, B. Kempnaers, Adaptive sleep loss in polygynous pectoral sandpipers. *Science* **337**, 1654–1658 (2012). [Medline](#)
22. H. Weimerskirch, M. Louzao, S. de Grissac, K. Delord, Changes in wind pattern alter albatross distribution and life-history traits. *Science* **335**, 211–214 (2012). [Medline doi:10.1126/science.1210270](#)
23. U. C. Mohanty, M. Mohapatra, O. P. Singh, B. K. Bandyopadhyay, L. S. Rathore, *Monitoring and Prediction of Tropical Cyclones in the Indian Ocean and Climate Change* (Springer, Dordrecht, Netherlands, 2014).
24. H. J. J. Jonker, T. Heus, P. P. Sullivan, A refined view of vertical mass transport by cumulus convection. *Geophys. Res. Lett.* **35**, L07810 (2008). [doi:10.1029/2007GL032606](#)
25. R. J. Spivey, C. M. Bishop, An implantable instrument for studying the long-term flight biology of migratory birds. *Rev. Sci. Instrum.* **85**, 014301 (2014). [Medline doi:10.1063/1.4854635](#)
26. R. J. Spivey, C. M. Bishop, Interpretation of body-mounted accelerometry in flying animals and estimation of biomechanical power. *J. R. Soc. Interface* **10**, 20130404 (2013). [Medline doi:10.1098/rsif.2013.0404](#)
27. R. J. Spivey, S. Stansfield, C. M. Bishop, Analysing the intermittent flapping flight of a Manx Shearwater, *Puffinus puffinus*, and its sporadic use of a wave-meandering wing-sailing flight strategy. *Prog. Oceanogr.* **125**, 62–73 (2014). [doi:10.1016/j.pocean.2014.04.005](#)
28. C. M. Bishop, R. J. Spivey, Integration of exercise response and allometric scaling in endotherms. *J. Theor. Biol.* **323**, 11–19 (2013). [Medline doi:10.1016/j.jtbi.2013.01.002](#)
29. S. Ward, C. M. Bishop, A. J. Woakes, P. J. Butler, Heart rate and the rate of oxygen consumption of flying and walking barnacle geese (*Branta leucopsis*) and bar-headed geese (*Anser indicus*). *J. Exp. Biol.* **205**, 3347–3356 (2002). [Medline](#)
30. F. A. Hartman, Locomotor mechanisms of birds. *Smithsonian Misc. Collect.* **143**, 1–91 (1961).
3331. P. S. Enger, Heat regulation and metabolism in some tropical mammals and birds. *Acta Physiol. Scand.* **40**, 161–166 (1957).

32. D. C. Dearborn, A. D. Anders, J. B. Williams, Courtship display by great frigatebirds, *Fregata minor*: An energetically costly handicap signal? *Behav. Ecol. Sociobiol.* **58**, 397–406 (2005). [doi:10.1007/s00265-005-0933-7](https://doi.org/10.1007/s00265-005-0933-7)
33. H. I. Ellis, G. W. Gabrielsen, Energetics of free ranging seabirds, in *Biology of Marine Birds*, E. A. Schreiber, J. Burger, Eds. (CRC Press, Boca Raton, FL, 2002).
34. C. M. Bishop, Heart mass and the maximum cardiac output of birds and mammals: Implications for estimating the maximum aerobic power input of flying animals. *Philos. Trans. R. Soc. London Ser. B* **352**, 447–456 (1997).  
[doi:10.1098/rstb.1997.0032](https://doi.org/10.1098/rstb.1997.0032)