2   **Exploring the relation between flapping behaviour and accelerometer signal during**

3   **ascending flight, and a new approach to calibration**

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13   We understand little about the energetic costs of flight in free-ranging birds; in part since current

14   techniques for estimating flight energetics in the wild are limited. Accelerometry is known to estimate

15   energy expenditure through body movement in terrestrial animals, once calibrated using a treadmill

16   with chamber respirometry. The flight equivalent, a wind tunnel with mask respirometry, is particularly

17   difficult to instigate, and has not been applied to calibrate accelerometry. We take the first steps in

18   exploring a novel method for calibrating accelerometers with flight energy expenditure. We collected

19   accelerometry data for Harris's Hawks *Parabuteo unicinctus* flying to varying heights up to 4.1 m over

20   a small horizontal distance; the mechanical energy expended to gain height can be estimated from

21   physical first principles. The relationship between accelerometry and mechanical energy expenditure

22   was strong, and while a simple wing flapping model confirmed that accelerometry is sensitive to both

23   changes in wing beat amplitude and frequency, the relationship was explained predominately by

24   changes in wing beat frequency, and less so by changes in amplitude. Our study provides initial, positive

25   evidence that accelerometry can be calibrated with body power using climbing flights, potentially

26   providing a basis for estimating flapping flight metabolic rate at least in situations of altitude gain.

27   **Keywords**: Harris Hawk, dynamic body acceleration, energetics, wing beat frequency, wing beat

28   amplitude

29

30   Volant birds can travel further and faster than animals employing other modes of locomotion. The

31   ability to fly underpins much of avian foraging and migratory behaviour, yet powered flight is

32   considered to require considerable energy expenditure (Schmidt-Nielsen 1972, Nudds and Bryant 2000,

33   Piersma 2011). Quantifying those costs is therefore essential to our understanding of bird biology.

34   Presently, however, we know very little about the true costs of flapping flight in unrestrained birds in

35   the wild (Elliott 2016, Hicks *et al.* 2017), particularly beyond cases of steady-state flight (Pennycuick

36   2008).

37   While wind tunnel experiments have proved invaluable for interrogating various aspects of flight

38   biology (Engel *et al.* 2010), training birds to maintain stationary flight in a current of air (Ward *et al.*

39   2002, Sapir and Dudley 2012) is difficult (Welch 2011), and habituating them to wearing a respirometry

40   mask at the same time in order to estimate energy expenditure is an additional problem. Furthermore,

41   the veracity of measurements taken during wind tunnel respirometry has been questioned (Engel *et al.*

42   2010). The mask and associated tubing imposes additional weight and drag on the bird, the wind tunnel

43   can elicit boundary effects (Rayner 1994), and captive animals are potentially less physically fit than

44   their wild contemporaries (Schwitzer and Kaumanns 2001). These issues may explain inconsistencies

45   between wind tunnel estimates of flight effort compared to field-based estimates (Liechti and Bruderer

46   2002). For example, the heart rate of wild geese during flight tends to be low (Bishop *et al.* 2015)

47   compared to that of geese during wind tunnel experiments (Ward *et al.* 2002). Furthermore, the tethering

48   effect of the mask limits the bird's freedom of movement, which may also serve to increase its energy

49   costs, and restricts investigation to scenarios of steady state, uni-directional flight. Other approaches for

50   measuring the energetic costs of flight include using energy models in conjunction with high-speed

51   kinematics (Askew and Ellerby 2007), but this is a further example of laboratory measurements, which

52   may yield quite different results to free flying birds in their natural environment. Many ecological and

53   behavioural questions can only be resolved in a natural setting.

54   One of the most promising approaches for investigating energy expenditure during flight in wild

55   animals is to attach a small data logger to the subject animal that records a proxy of energy expenditure.

56   Calibrating the proxy with energy expenditure in the laboratory enables quantified estimates of energy

57   expenditure to be calculated from measures of the proxy recorded in the field (Sapir *et al.* 2010). For

58   example, calibrations between heart rate and energy expenditure obtained for two species of geese

59   (Ward *et al.* 2002) were applied to heart rate recordings of Bar-headed Geese *Anser indicus* on migration

60   from Mongolia to India through the Himalayas, estimating energetic savings for these birds from flying

61   close to the ground compared to ascending progressively across the mountain range (Bishop *et al.* 2015).

62   However, applying such 'biologging' to quantify energy expenditure in birds while flying is in its

63   infancy (Guillemette *et al.* 2012, Elliott *et al.* 2013, Elliott *et al*. 2014, Weimerskirch *et al.* 2016) with

64   few proxy calibrations available. This is, at least in part, because calibrating energetics proxies for flying

65   birds is very difficult, given the logistics, for example, of wind tunnel respirometry.

66   Accelerometers are used as biologging devices that record the acceleration of the body of the animal.

67   Both in theory (Gleiss *et al.* 2011) and in practice (Wilson *et al.* 2006), recordings from accelerometers

68   attached to a central point on an animal's body relate well to the levels of movement of that animal, and

69   in turn its energy expenditure during periods of activity. A now commonly used derivative of

70   accelerometry data used as a proxy for energy expenditure is termed dynamic body acceleration (DBA)

71   (Halsey *et al.* 2011, Qasem *et al.* 2012). During flapping flight, acceleration of the animal's body, and

72   thus DBA, is affected by variation in flapping behaviour (Halsey *et al.* 2009, Spivey and Bishop 2013,

73   Bishop *et al.* 2015, Weimerskirch *et al.* 2016) which is described predominantly by wing beat

74   frequency, wing beat amplitude or a combination of the two (Rayner 1999). Strong relationships

75   between rate of energy expenditure and DBA have been found in a diversity of cursorial birds such as

76   Red Jungefowl (chickens) *Gallus gallus*, Great Cormorants *Phalacrocorax carbo* and Macaroni

77   Penguins *Eudyptes chrysolophus* (Wilson *et al.* 2006, Green *et al.* 2009, Halsey *et al.* 2009). Yet to date

78   there has been no empirical calibration of accelerometry with energy expenditure for birds during flight.

79   The three-dimensional nature of bird flight means that the relationship between DBA and energy

80   expenditure cannot be easily predicted from simple theoretical considerations: birds could switch

81   between different flapping modes as they fly on different slopes, leading to difficult to predict effects

82   on DBA. Our study takes the first steps to address this. We provide the first experimental relationship

83   between accelerometry (as DBA) and rate of energy expenditure (as climb power is associated with the

84   gain in potential energy) in a volant animal, by using variation in climbing slope during free flights to

85   enable climb power to be estimated from physical first principles. These experiments also enabled us

86   to investigate what aspects of wing kinematics (e.g. increased flapping frequency or flapping amplitude)

87   drive power output in this particular flight scenario and how effectively DBA can describe these

88   kinematics.

89   We fitted Harris's Hawks *Parabuteo unicinctus* with accelerometers and encouraged them to undertake

90   short flapping flights that varied in the height gained between the two falconers. The extra energy (climb

91   power) expended by the bird in achieving these various heights was calculated from physical first

92   principles as the product of the mass of the bird, gravitational acceleration, and the rate of increase in

93   height (Askew *et al.* 2001, Berg and Biewener 2008). This enabled us to test for and investigate

94   relationships between energy expenditure (as climb power) and DBA in birds without heavy logistical

95   burdens, outside the laboratory, flying freely and without restricting the animals such as obliging them

96   to wear a respirometry mask. We further explored our findings by investigating the relationships

97   between DBA and bird kinematics both empirically and using simple wing flapping models based on

98   sinusoidal waves (Spivey and Bishop 2013); the modelling helps to clarify some common

99   misunderstandings about how cyclical body movement impacts measures of body acceleration.

100   **Methods**

101   *Experimental set-up*

102   We collected data from five (one male and four female) Harris's Hawks weighing between 0.84 – 1.03

103   kg, at the Hawk Conservancy Trust (HCT) in Andover (UK). Data were collected in the summer and

104   autumn of 2016, under approval of the ethics committee of the University of Roehampton.

105   We encouraged the hawks to fly to six different heights (range: 0 – 4.1 m, Figure 1 and

106   From the height gained by a hawk during each flight (

107   Table **1**), along with the duration of the flight and the mass of the bird, mean climb power during the

108   flight can be calculated by:

109    $$\text{Climb power (Js}^{-1}\text{)} = \frac{\text{mass (kg)} \times \text{gravitational acceleration (9.81ms}^{-2}\text{)} \times \text{height gained (m)}}{\text{flight duration (s)}}$$

110

Table **1**) while covering only a small horizontal distance (4.1 m). Lured by morsels of chicken (weighing 1 - 2 g), the birds flew back and forth from a falconer on the ground to a falconer standing at different heights on flights of steps up to a balcony. Their body mass therefore increased slightly with each flight; we accounted for this in our analyses by assuming that each piece of food weighed 1.5 g. Each height condition was randomised, and repeated approximately three times per bird. Wind speed was measured with an anemometer and never exceeded 0.3 m/s so we considered wind to be negligible for our experiment.

We placed a small accelerometer (9.3 g, ~1% of body mass; GCDC USB accelerometer X16-4) on the lower section of the Harris's Hawk's back, towards the rump where it would not interfere with wing movement (Figure 2). The accelerometer was set to record at 50 Hz (around 10-fold the wing beat frequency of Harris's hawks). Similar to some previous studies of bird flight power and kinematics (Pennycuick *et al.* 1989, Askew *et al.* 2001, Berg and Biewener 2008), flight durations were short, averaging 1.7 s (± one sd: 0.3).

Video recordings

We video recorded the flight of the birds with a *Nikon Coolpix AW110* camera, hand-held by a researcher standing on the ground, perpendicular to the bird's trajectory. The video was used subsequently to check flight durations and times, synchronise the flight times with the accelerometry data, and note any aberrant behaviours by the birds during the flights (e.g. bird not flying to the target); those flights (n = 6 from three birds) were removed prior to analysis. We used the programme IGOR Pro (Wavemetrics Inc., Portland, OR, USA, 2000, *version 6.3.5*) with the Ethographer package (Sakamoto *et al. 20*09) in concert with the video footage, to extract the acceleration traces representing each flight.

Estimating climb power

From the height gained by a hawk during each flight (

135   Table **1**), along with the duration of the flight and the mass of the bird, mean climb power during the

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138

139 Table 1. Height gain and flight distance represented by each experimental condition. Average height
140 varied slightly within each condition due to slight variations in the stance adopted by the two falconers.

Flight condition	Mean height gain (and range) (m)	Mean flight distance (and range) (m)	Mean flight duration and range (s)	# Birds (and # flights)
H1	0	4.1	1.6 (1.2 – 2.2)	5 (14)
H2	1.3 (1.2 – 1.6)	4.3 (4.3 – 4.4)	1.6 (1.2 – 2.4)	5 (17)
H3	1.8 (1.6 – 2.0)	4.5 (4.4 – 4.6)	1.6 (1.3 – 2.6)	5 (19)
H4	2.5 (2.3 – 2.9)	4.8 (4.7 – 5.0)	1.7 (1.3 – 2.2)	4 (13)
H5	3.8 (3.5 – 4.2)	5.6 (5.4 – 5.9)	1.9 (1.5 – 2.5)	4 (12)
H6	4.1 (3.9 – 4.3)	5.8 (5.7 – 5.9)	2.1 (1.7 – 2.5)	5 (13)

141

142 *Accelerometry data analysis*

143 Accelerometers measure both dynamic (body movement) and static acceleration (gravity) (Gleiss *et al.*
144 2011), and the tag model we used recorded acceleration along three orthogonal axes (heave, surge and
145 sway) measured in absolute g (1 g = 9.81 m s^{-2}). Thus, the acceleration of the bird's body due to the
146 movement of its wings could be determined by recording the acceleration experienced by the data logger
147 attached to a fixed point on the body, such as the lower back, and then from those data by extracting an
148 approximation of absolute g due only to dynamic acceleration (Gleiss *et al.* 2011, Halsey *et al.* 2011).
149 This extraction was achieved in our study by removing an approximation of the static acceleration
150 calculated as the mean of each accelerometry axis over the duration of the flight, similar to employing
151 a running mean (Shepard *et al.* 2008). Preliminary analysis showed that we found a stable DBA within
152 the average flight duration of the hawk. The resulting absolute dynamic values were then summed to
153 produce the derivation termed 'overall dynamic body acceleration', hereafter, DBA.

154 *Calculating flapping kinematics from the accelerometry data*
155 All the flapping analyses were implemented in Matlab *v.7.9.0.529*. We projected the accelerometer
156 signal along one dimension. This dimension was defined as the major flapping axis of the Harris's
157 Hawk, determined independently for each flight through principal component analysis of the three-
158 dimensional accelerometer recordings. Next, we applied a cubic spline interpolation of this
159 accelerometer signal with a temporal resolution of 250 fixes per second (5 times the original resolution
160 of the data). This step was included because the temporal resolution for detecting wing beat frequency
161 is limited by the temporal discretisation of the data, however the accelerometer signal itself carries
162 sufficient information for a much more accurate estimation, because the signal is repeated over multiple
163 flapping cycles. This information was integrated in the subsequent steps of analysis.

164   We estimated wing beat frequency by computing a temporal autocorrelation of the interpolated

165   accelerometer signal and by detecting the time lag that corresponded to the second highest peak in the

166   autocorrelation function (the first highest peak is the trivial autocorrelation maximum at zero delay).

167   This time lag gave the time period T of one flapping cycle, the wing beat frequency being $1/T$. In four

168   flights of one bird, the second highest peak in the autocorrelation function was of similar height to the

169   third highest peak and its position indicated incorrect values of wing beat frequency (higher than 8 Hz

170   or lower than 4 Hz, clearly different from what we could observe in the video footage). For these four

171   flights, we manually forced selection of the third highest peak.

172   Acceleration amplitude along the major flapping axis is a measure of the amplitude of acceleration of

173   the bird's body (Usherwood *et al*. 2011, Spivey and Bishop 2013), which in turn is assumed to result

174   predominantly from wing flapping. Acceleration amplitude was estimated directly from the local

175   maxima and local minima of the interpolated accelerometer signal. As the accelerometer signal had

176   multiple local maxima and minima, some of which were determined by noise (or by higher harmonics

177   of wing movements), we limited the analysis to local maxima and minima that were also global maxima

178   or minima within a time window of 70% of one flapping cycle. As an aggregate measure of amplitude

179   of acceleration during the flap cycles over the entire flight, we kept the value that corresponded to the

180   80th percentile of the absolute amplitude of local maxima and minima, under the assumption that this

181   would be only minimally sensitive to extreme variations of amplitude associated with take-off and

182   landing. Acceleration amplitude was used to estimate the movement amplitude of the bird's body

183   (hereafter termed 'body movement amplitude', cm) by considering the body to fluctuate over time

184   following a pure sine wave (Spivey and Bishop 2013). Body movement amplitude is assumed to be

185   proportional to wing beat amplitude and thus an indirect measure of it (Hedrick *et al.* 2004, Usherwood

186   *et al.* 2011, Taylor *et al*. 2017) (supplementary material includes a Matlab code to calculate the wing

187   beat amplitude and body movement amplitude).

188   From the measured values of DBA we calculated an estimated measure of 'body power', or the power

189   produced by flapping. Under relatively well supported assumptions of sinusoidal flapping, body power

190   is proportional to the amplitude of the accelerometer signal and inversely proportional to the squared

191   wing-beat frequency (see for instance Spivey and Bishop 2013), so here we defined body power simply

192   as body power $= \frac{DBA^2}{WBF}$ (this is analogous to other definitions of body power based on RMS (Root Mean

193   Square) contrast of accelerometer signal: RMS contrast and DBA are both proportional to the amplitude

194   of the sinusoidal flapping signal, body power $= \frac{RMS^2}{WBF}$)

195   *Statistical analyses*

196   Statistical analyses focussed on general linear models implemented in the programming environment R

197   3.4.0 (Team 2013), using the *lme4* package. In different models, DBA (g), climb power (Js^{-1}) and climb

198   energy per wingbeat (*J*) were the outcome variables, with either body movement amplitude (*cm*), wing

199   beat frequency (*Hz*), climb power or body power (*Js^{-1}*) as single predictor variables. All models included

200   bird ID as a random factor, allowing slope intercept and gradient to differ for each bird. We then

201   performed a cross-validation analysis to quantify the predictive validity of our model calibrating DBA

202   with climb power. Using a jack knife approach, we simulated the scenario of estimating climb power

203   from measures of DBA obtained from a new individual. We excluded one bird from the dataset in

204   generating the relationship between climb power and DBA, and then used that relationship to compare

205   climb power against DBA-predicted climb power, for 10 randomly selected values of DBA. Mean

206   absolute and mean algebraic percentage error was calculated for these 10 samples. This process was

207   repeated for all five birds and overall means were then calculated.

208   R^2 values for mixed effects models were calculated following the method of Nakagawa and Schielzeth

209   (2013) using the MuMIn package. Because the *p* value is typically highly imprecise, here we consider

210   it to be only a tentative indication of the strength of evidence for observed patterns in the data (Fisher

211   1959, Boos and Stefanski 2011, Halsey *et al.* 2015). To enhance interpretation of the *p* value, we have

212   supplemented reporting the *p* values with further information following the three key recommendations

213   of the American Statistical Association (Wasserstein and Lazar 2016), further explained in Altman and

214   Krzywinski (2017), which enable assessment of the strength of evidence for the falsehood of the null

215   hypothesis. First, we provided estimates of the false discovery rates associated with each null hypothesis

216   – the expected proportion of the rejected null hypotheses that are false rejections. These were calculated

217   based on predicted statistical power of 80% and the heuristic for low-throughput testing recommended

218   by Altman and Krzywinski (2017) to predict the proportion of tests that are truly null: 50% for primary

219   research questions and 75% for secondary research questions. Second, we calculated the upper bound

220   for the Bayes factor (Sellke *et al.* 2001, Boos and Stefanski 2011) – the largest possible Bayes factor

221   over any (reasonable) choice of the prior distribution for the alternative hypothesis. The value represents

222   the ratio of average likelihoods under the alternative and null hypotheses, i.e. a quantification of the

223   extent to which the alternative hypothesis (that the effect size is not null, i.e. not 0), is more likely.

224   Third, all our data figures include 95% confidence intervals, both standard and bootstrapped (Loftus

225   1993, Lavine 2014).

Results

Empirical data analysis

228   Five Harris's Hawks undertook a total of 88 flights that were included in the analyses. Cleveland plots

229   indicated no clear outliers in the data set. The observations:covariates ratio was never lower than 24 for

230   the models constructed, which is acceptable (Zuur *et al*. 2013). There was no relationship between the

231   Pearson residuals and the fitted values from this study's main model: DBA ~ climb power + [bird_ID].

232   None of the Cook's distances were outliers. The relationship between observed data and fitted data for

233 this model was approximately unitary. Plots of Pearson residuals against each model covariate in this
234 study's analyses did not indicate any obvious non-linearity (48).

235 To generate relationships between rate of energy expenditure and DBA, we plotted mean DBA against
236 estimated climb power (Figure 3); the plot indicated that they correlate positively. The R^2 values for
237 climb power regressed against DBA for each bird separately ranged between 0.58 and 0.80. A linear
238 mixed model to predict DBA from climb power, including bird identity as a random factor, indicated a
239 strong relationship (Table 2). To quantify the predictive accuracy of the relationship between climb
240 power and DBA, we performed a cross-validation analysis. Overall mean absolute error was $19.22 \pm$
241 1.16% (range of mean absolute error: $0.22 - 68.08\%$), while overall mean algebraic error was $-4.00 \pm$
242 1.96% (range of mean algebraic error: $-68.08 - 42.41\%$).

243 Consequently, we then explored the relationships between key aspects of wing kinematics and climb
244 power, and how effectively DBA described those wing kinematics (Table 2). The flight kinematic
245 variables we investigated at this point were body movement amplitude (a proxy for wing beat
246 amplitude) and wing beat frequency. DBA was related statistically significantly but not strongly to body
247 movement amplitude (Figure 4A), and related more strongly to wing beat frequency (Figure 4B).
248 Similarly, climbing power was related statistically significantly but not strongly to body movement
249 amplitude (Figure 4C), and more strongly to wing beat frequency (Figure 4D). Consequently, there was
250 a fairly strong positive relationship between climb energy per wing beat and climb power (Figure 4E).
251 Finally, climb power was regressed against $\frac{DBA^2}{WBF}$, which is the theoretical relationship derived by Spivey
252 and Bishop (2013) for body power perceived by the body-mounted accelerometer (Figure 4F), but the
253 relationship had a weaker correlation (marginal R^2) than that for DBA, or even wing beat frequency,
254 alone.

255

Table 2. Model outputs, accounting for repeated measures within each bird, investigating the relationships between dynamic body acceleration (DBA, *g*), climb power (*Js*⁻¹), wing beat frequency (WBF; Hz), body movement amplitude (BMA; cm), climb energy per wingbeat (Energy per wingbeat; *J*) and body power (*Js*⁻¹). Marginal R^2 describes the proportion of variance explained by the fixed factor(s) alone; Conditional R^2 describes the proportion of variance explained by both the fixed factor(s) and the random factor (bird ID). eFDR = estimated false discovery rate. The Bayes factor bound calculates the upper bound of the Bayes factor based on the reported *P* value, and indicates the ratio of the likelihood that the alternative hypothesis is true against the likelihood that the null hypothesis is true. See the main text for further details.

Associated Figure	Model	Slope (± se)	Marginal R^2	Conditional R^2	*P* value	eFDR (%)	Bayes factor bound
Figure 3	DBA ~ climb power	0.092 ± 0.009	0.54	0.64	< 0.001	0.12	53
Figure 4A	DBA ~ BMA	0.28 ± 0.067	0.17	0.17	<0.001	0.37	53
Figure 4B	DBA ~ WBF	1.88 ± 0.27	0.38	0.52	<0.001	0.37	53
Figure 4C	Climb power ~ BMA	1.46 ± 0.651	0.06	0.19	0.02	6.98	5
Figure 4D	Climb power ~ WBF	17.8 ± 2.0	0.48	0.64	<0.001	0.37	53
Figure 4E	Energy per wingbeat ~ climb power	0.173 ± 0.012	0.61	0.84	<0.001	0.37	53
Figure 4F	Power ~ climb power	6.71 ± 0.727	0.32	0.62	<0.001	0.37	53

Modelled data analysis

Superficially, one might conclude that changes in wing beat frequency will not be recognised by changes in DBA (or related measures such as RMS) because DBA depends only on the amplitude of the acceleration profile and not its frequency (Fig. 5). The total DBA of a flapping cycle corresponded to the area shaded in grey in Figure 5a. If the bird produced an identical accelerometer profile, but flapped at double the frequency (Fig.5b), the total DBA of a flap cycle would now be reduced to one half the original, but there would now be two identical flapping cycles per unit of time, so that average DBA calculated across multiple flap cycles would be identical (see the appendix for a proof).

However, it would be wrong to conclude that the profile presented in Figure 5b would result from the bird increasing its wing beat frequency while maintaining constant wing beat amplitude. There is a crucial and fundamental distinction to be made between the amplitude of the signal in the recorded acceleration trace (*g*) and the amplitude of the bird's wing flaps (*cm*). The amplitude of the accelerometer profile carries information about both the amplitude and the frequency at which the bird flaps its wings. A larger flapping amplitude for a given wing beat frequency registers higher acceleration

280   values and, for a given flapping amplitude, a higher wing beat frequency will register higher

281   acceleration values. Simply put, a flapping wing must speed up and slow down more rapidly if it is

282   moving further per unit time, or flapping more frequently. Thus, even if inspection of the profile of the

283   bird's body movements in cm (in reaction to its wing beats) does not show any change in gain in

284   response to a change in its wing beat frequency (Figure 6a), DBA derived from an accelerometer

285   instrumented to the bird's back should nonetheless recognise this variation in flapping behaviour

286   (Figure 6b).

287

288   **Discussion**

289   During flapping flight, to gain height birds must expend energy. We took advantage of this fact to

290   generate relationships between the output of an accelerometer and the rate of mechanical energy

291   expenditure of volant birds by instrumenting the accelerometer to the back of Harris's Hawks while

292   they undertook ascending flights.

293   *The relationship between climb power, DBA and wing kinematics*

294   Although our experimental design induced the birds to ascend to different heights and thus expend

295   different total amounts of energy, this did not ensure that they would vary their mean climb power.

296   Fortunately, however, climb power did vary, providing variation that might covary with DBA. DBA

297   derived from the recorded accelerometry data during these flights related to climb power positively and

298   strongly (Figure 3), characterised by an overall mean absolute prediction error of less than 20%, and

299   overall mean algebraic error (giving an indication of the predictive error if mean climb power across

300   multiple birds was estimated) of -4%. This augurs well for the future use of accelerometers to estimate

301   energy expenditure in volant birds.

302   Variation in DBA (due to variation in climb power) was explained more by changes in wing beat

303   frequency (Fig. 4b) than by changes in wing beat amplitude (measured in terms of body movement

304   amplitude; Figure 4a). The birds' increase in wing beat frequency to increase power was clear (Fig. 4d)

305   despite the variation in wing beat frequency being small (across all birds typically ranging from about

306   4.7 to about 5.8 Hz). Our wing flap models demonstrated that DBA can be sensitive to both changes in

307   body movement amplitude and wing beat frequency (Fig. 6); it appears that the Harris's Hawks enacted

308   relatively small changes in wing beat frequency in order to generate relatively large changes in climb

309   power. This has been quantified once before, in Bar-headed Geese (Bishop *et al*. 2015). Small increases

310   in wing beat frequency might be expected to associate with relatively high power costs given that, for

311   horizontal steady flight, power requirement should be proportional to wing beat frequency cubed

312   (Lilienthal 2001). However, the wing beat frequency of the Harris's Hawks leaves quite a lot of

313   variation in DBA and climb power unexplained, and a regression of climb energy expended per wing

beat against climb power, while strong, includes a fair amount of variability (Figure 4E). Our wing flap models indicated that DBA is likely to be somewhat sensitive to changes in wing beat frequency, leaving the possibility that the birds made other changes to their flight kinematics over and above wing beat frequency and wing beat amplitude to change their climb power. Similarly, Frigatebirds *Fregata spp.* hold wing beat frequency fairly constant yet heart rate per wing beat (a proxy of power output per wing beat) varies substantially during the course of a flight (Weimerskirch *et al.* 2016). In both these cases, one possibility is that the birds change stroke plane angle, as has been reported in pigeons during short, height-gaining flights where power output per wing beat was higher when the required flight angle (and hence predicted power) was greater (Berg and Biewener 2008).

The calculated mean maximum climb power exhibited by the Harris's Hawks during flights in the present study was about 25 Js^{-1}, which is similar to that reported for 2s climbing flights by the same species in an earlier study (Pennycuick *et al.* 1989; their Figure 7). This is, of course, only a part of the total power costs of flight for the bird, which include muscle contractions of the wings and other body parts, the costs to overcome drag and basic lift, and basal metabolic rate. For example, during flight a bird's basal metabolic rate could constitute 4 to 10% of its total metabolic costs (Nudds and Bryant 2000, Piersma 2011), and flight muscle efficiency is typically less than 20% (Rayner 1999). In reality, total power during a flight is likely to be many times higher than calculated climb power, and could vary with mechanical power (Rayner 1999, Pennycuick 2008, Engel *et al.* 2010). The gross energy costs for a human to jump horizontally is around 8-fold greater than the energy expenditure calculated from physical first principles (Halsey *et al.* 2016). Similarly, the gross energy costs to ascend and descend a ladder are around 13-fold greater (Halsey *et al.* 2016). Nudds and Bryant (2000) reported strong inter-specific correlations between gross power output and body mass during flight in birds based on a literature review of empirical studies. For short flights, their relationship predicted gross power to be 250 J s^{-1} for a 1 kg bird, which is about 10 times the maximum mean climb power exhibited by the hawks in the current study. It should be borne in mind that shorter flights are particularly energetically demanding, due to take-off costs (Nudds and Bryant 2000) and the higher power costs associated with slower flight speeds (Engel *et al.* 2010). Relationships between DBA and climb power could be a valuable platform for estimating flight metabolic rate as our understanding of a bird's internal power costs becomes clearer, and even without estimates of internal power costs, such relationships should reflect relative changes in energy expenditure.

The precise mathematical relationship between amplitude of body movement and accelerometer signal can be derived as follows. Consider the case of a bird which has flapping described by a pure sine wave, such that the *z* position of its body (to which the accelerometer is attached) fluctuates over time from a minimum height -*B* to a maximum height +*B*, with period *T*. In this case we have

348     $z(t) = B\sin(Wt)$ where we used $W = \dfrac{2p}{T}$ to represent the angular velocity and simplify the notation.

349   The accelerometer does not directly record the bird's body position at any given time t, $z(t)$, but simply

350   its acceleration, that is, the second derivative of body position. Indicating this acceleration with a capital

351     $Z(t)$ we have:

352     $Z(t) = \dfrac{d^2 z}{dt^2} = BW^2 \sin(Wt)$

353   Importantly, the accelerometer profile describes a sine wave, with the same period or frequency as the

354   body (the $\sin(\omega t)$ part is identical in the two equations), but where the amplitude has now changed from

355   B (a function of body movement amplitude only) to $B\omega^2$ (a function of both body movement amplitude

356   and wing beat frequency).

357   Under these assumptions, we can directly calculate the amplitude of body movements (cm) from the

358   amplitude and frequency of flapping recorded by the accelerometer. For example, in our data we have

359   typical values of accelerometer amplitude $A \approx 5\ g$, or $A = 5$ x 9.81 ms^{-2}, and $T \approx 0.2$ s, from which $\omega =$

360   2 x π / 0.2 s^{-1} and $B = A/\omega^2 = 5$ x 9.81 / $(2$ x π / $0.2)^2$ m $= 0.05$ m $= 5$ cm. (See also Spivey and Bishop

361   2013 for a more accurate and complete analysis of the sinusoidal model).

362   Real birds are unlikely to flap with a perfect sinusoidal profile. However, as long as the flapping profile

363   is periodic, it can be described as the sum of multiple sine functions by Fourier series approximation

364   and the same mathematical reasoning above holds independently for each of the harmonics.

365   *Improving the DBA-power relationships*

366   Our experiments included sources of potential error that could increase noise in the relationships

367   reported. Defining and discerning the start and end of each flight is an imperfect endeavour, resulting

368   in some degree of inconsistency and inaccuracy in measuring flight duration and selecting the associated

369   accelerometry trace. The exact height gained by a bird was also subject to error due to variation within

370   each height condition of the exact body postures and hand placements of the falconers, though most of

371   this variation was accounted for by inspecting the video footage. Because of the short duration of the

372   flights, variation in how take-off and landing was incorporated into calculations for each flight could

373   instigate considerable noise to the reported relationships. We investigated whether removing the start

374   and end of the accelerometry trace for each flight improved the relationship specifically between DBA

375   and climb power. We progressively shortened the analysed flights by 0.1 s intervals at both ends

376   simultaneously (up to 0.3 s at each end), and found that this tended to slightly weaken the relationship.

377   This process therefore provided no evidence that our assessment of the flight start- and end-points were

378   inaccurate. If the birds could be trained to undertake flights incorporating greater height gain while

379   maintaining the short horizontal flight distance, this might serve to improve the DBA-power

relationship, unless for extended flights of this type the birds choose to maintain a more consistent power output between height conditions. We were able to position the logger on the back at a consistent point within and between individual birds, which is important to reduce noise-based variation in the relationships between climb power, DBA and flight kinematics between birds. The results of the present study have confirmed that DBA depends partly on body movement amplitude (Sapir *et al.* 2010, Bishop *et al*. 2015), which in turn will depend on logger positioning since differing locations may influence the degree of oscillation experienced by the logger. Thus, it is possible that certain logger positions return stronger predictive relationships between climb power and DBA or body movement amplitude than others (Halsey *et al*. 2008).

Our data indicate considerable variation in the relationship between DBA and climb power among individuals (Figure 3). Such variation in energy-proxy relationships among individuals is typical e.g. (Halsey and White 2010, Green 2011, Halsey *et al.* 2011), and is ripe for investigation with detailed kinematic data. Inter-individual variability can be recognised statistically in the errors associated with estimates of energy expenditure at the group level (Green *et al*. 2003, Green 2011, Lyons *et al.* 2013), where mean values for the group tend to be accurate (e.g. Halsey *et al*. 2007).

The future for accelerometry to investigate flight energetics

We need ways to estimate energy expenditure in free-flying birds, and other volant animals, at a high resolution, and non-invasive instrumentation of data loggers is currently the most tractable option (though surgical implants may be preferential for long term deployments (White *et al*. 2013)). Researchers have only just begun to apply accelerometry measurements to estimate the energy expenditure of flapping flight. Bishop *et al.* 2015 showed that in Bar-headed Geese migrating through the Himalayas, variations in heart rate and accelerometry closely track each other (their Figure 1); given that heart rate correlates with rate of oxygen consumption in this species (Groscolas *et al.* 2000), we can reasonably conclude that accelerometry can predict the power costs of flapping flight, at least in geese. Heart rate also correlates with accelerometry metrics in airborne Griffon Vultures *Gyps fulvus* (Duriez *et al*. 2014), while Hicks *et al.* (2017) demonstrated that accelerometry relates to power output in European Shags *Phalacrocorax aristotelis*. The current study supports these conclusions, this time providing direct evidence of a relationship between DBA and mechanical power, the latter derived from first principle calculations. Further work is required to produce calibrations for application in the field. In situations where birds undertake extended periods of ascending flapping flight e.g. (Clarke *et al.* 2007, Bishop *et al*. 2015), which may have an important effect on their energy stores or fatigue, the approach presented in the current study can be particularly valuable.

Acknowledgements

425

426   **Data accessibility**

427   The datasets supporting this article, as well as a Matlab code for running our wingbeat analysis (as

428   described in our methods section) have been uploaded to Figshare.com.

429

430   **Competing interests**

431   We have no competing interests.

432   **Author contributions**

433   Data collection, analysis, interpretation of data, first draft, review (TvW, AP, LH). Data collection,

434   analysis, interpretation of data, review (PC, CB). Interpretation of data, review (RW, CM). All authors

435   have approved final version of the manuscript and have agreed to be accountable for all aspects of the

436   work in ensuring that questions related to the accuracy or integrity of any part of the work are

437   appropriately investigated and resolved.

438

Figure Legends

Figure 1 Schematic diagram of the experimental setup. (H1 = 0 m height gain; H6 = 4.5 m height gain; see main text for further details). For each height condition the bird flew from falconer 1 to falconer 2.

Figure 2 Attachment (left) and location (right) of the accelerometer, placed on the back of the Harris's Hawk using surgical tape. The accelerometer was protected from rain and dust by a thin plastic film.

Figure 3. Regressions of mean dynamic body acceleration (DBA) against mean climb power during short flights by Harris's Hawks ($N = 5$). The plotted data represent single values ($n = 88$), colour- and shape-coded to identify each bird. Colour- and style-coded lines of best fit are shown; NB that one best fit line (green, long dash) substantially obscures another (olive, short dash). Bird 1, red full and circle symbols, $R^2 = 0.80$, Bird 2, olive short dash and triangle symbols, $R^2 = 0.58$, Bird 3, green long dash and squared symbols, $R^2 = 0.64$, Bird 4, blue wide dash and plus symbols, $R^2 = 0.70$, Bird 5, mauve stippled and cross squared symbols, $R^2 = 0.66$.

Figure 4. Relationships between flight kinematics, dynamic body acceleration (DBA) and estimates of climb power during short flights by five Harris's Hawks ($n = 88$). In each panel, the black line represents the line of best fit returned from a linear mixed model that included bird identity as a random factor. The grey dashed lines indicate the 95% confidence interval around the line of best fit derived from standard calculations, while the grey stippled lines indicate the 95% confidence intervals derived from a bootstrap procedure based on 200 iterations.

Figure 5. The average dynamic body acceleration (DBA) per unit time only depends on the amplitude of the accelerometer signal and not on its frequency. (a) Idealised flapping profile recorded by the accelerometer. The average DBA of a flapping cycle corresponds to the area of the shaded region, divided by the length of the flapping cycle (in this example 0.2 s). (b) Accelerometer profile identical to the one in (a), but with double the frequency. The shaded area in each cycle is now only half the area in (a), but there are now twice as many cycles per unit time, so that the average DBA is unchanged.

Figure 6. Modelled relationships between body movement, acceleration amplitude and wing beat frequency. (a) Two hypothetical flapping profiles, here exemplified by sinusoidal curves, having exactly the same amplitude (in cm of body oscillations) but different frequencies (black curve: 5.5 Hz; red dashed curve: 4.125 Hz). The body movements exemplified in (a) produce acceleration profiles (in units of g) with identical frequencies (b), but the amplitude has changed - faster body movements produce higher acceleration amplitudes for the same body movement amplitudes.

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