

RESEARCH ARTICLE

Acceleration as a proxy for energy expenditure in a facultative-soaring bird: Comparing dynamic body acceleration and time-energy budgets to heart rate

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Abstract

1. In animal ecology, energy expenditure is used for assessing the consequences of different behavioural strategies, life-history events or environments. Animals can also influence energy expenditure through instantaneous behavioural responses to their external environment. It is therefore of interest to measure energy expenditure of free-ranging animals across seasons and at high temporal resolutions. Heart rate has historically been used for this, but requires invasive surgery for long-term use. Dynamic body acceleration (DBA) is an alternative proxy for energy expenditure that is simpler to deploy, yet few studies have examined how it performs over extended time periods, or for species using different locomotory modes, especially passive modes like soaring flight.
2. We measured DBA alongside heart rate in free-ranging lesser black-backed gulls, a seabird that moves using flapping flight, soaring and walking, and rests on both land and water. Our objectives were to compare the relative changes in DBA and heart rate among and within behaviours and to examine how accelerometers can be used to estimate daily energy expenditure by comparing DBA to time-energy budgets (TEBs).
3. DBA and heart rate were sampled concurrently at 2.5- and 5-min intervals throughout the breeding season, though measurements were not exactly synchronised. Behaviour was identified from accelerometer measurements, and DBA and heart rate were averaged over bouts of consistent behaviour. Heart rate was converted to metabolic rate using an allometric calibration, after confirming its fit using metabolic measurements taken in captivity and values from existing literature.
4. Both proxies showed similar changes among behaviours, though DBA overestimated costs of floating, likely due to waves. However, relationships between

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DBA and heart rate were weak within a behaviour mode, possibly due to the lack of synchrony between proxy measurements.

5. On daily scales, DBA and TEBs perform comparably for estimating daily energy expenditure. Accelerometry methods deviated from a 1:1 relationship with heart rate because acceleration could not measure variation in resting metabolic costs.
6. We conclude DBA functions well for detecting energy expenditure arising from activity costs, including during soaring flight. We discuss scenarios where one method (DBA vs. TEBs) may be preferred over the other.

KEYWORDS

biologging, energetics, lesser black-backed gull, locomotion, metabolic rate, seabird, soaring, tri-axial acceleration

1 | INTRODUCTION

Living organisms constantly expend energy. Energy is used to fuel resting processes such as basal metabolism, thermoregulation, production (e.g. growth, body maintenance) and digestion, as well as physical activity (e.g. locomotion). The balance between energy gain and use determines an individual's ability to survive, grow and reproduce, and thus energy is considered to be a unifying currency in biology (McNab, 2002; McNamara & Houston, 1996; Ricklefs, 1996). In animal ecology, determining patterns of daily or seasonal energy expenditure can reveal the consequences of inhabiting different environments or employing different behavioural strategies (Anderson & Jetz, 2005; Careau & Garland, 2012), as well as exploring how energy requirements vary throughout the year or between life-history stages (Dunn et al., 2020; Rotics et al., 2016). Organisms can also influence their daily energy expenditure (DEE) through fine-scale responses to their environment. For example, animals may be able to reduce energy expenditure by avoiding landscape features that increase locomotion costs (Shepard et al., 2013), or by moving at times when environmental conditions facilitate passive movement (Gibson, 2003; Shamoun-Baranes et al., 2016). As such, measuring metabolic rates of free-ranging animals at both high temporal resolutions and continuously throughout the annual cycle provides a mechanistic explanation of the internal and external drivers influencing the ecology, behaviour and evolution of species (Tomlinson et al., 2014).

Several proxies have been developed to estimate metabolic rates in free-ranging animals, including mass loss, isotopic turnover (e.g. doubly labelled water technique), heart rate (f_h), dynamic body acceleration (DBA) and time-energy budgets (TEBs; reviewed by Elliott, 2016). Of these techniques, only f_h and DBA have the capacity to both detect near-instantaneous changes in energy expenditure (i.e. resolutions of several seconds; Bishop et al., 2015), while being remotely monitored so that energy expenditure can be continuously measured at seasonal or annual time-scales (Flack et al., 2016; Green, Boyd, et al., 2009).

Measuring f_h in the wild for long periods typically requires surgical implantation, making it invasive and logistically challenging in field conditions. The f_h method relies on Fick's equation, which states that the rate of oxygen consumption (\dot{V}_{O_2}) is equal to the product of heart rate and the O_2 consumed by the animal per heartbeat. Heart rate is therefore only a partial measure of oxygen uptake from the blood, thus the relationship between f_h and \dot{V}_{O_2} in an individual can change with, for example, body mass, heart volume, activity mode and stress (Green, 2011). As such, derivation of energy estimates from f_h typically requires species and activity-specific calibrations (Green, 2011). When measured alone, f_h provides limited information regarding activity mode, though coarse identification of resting and active periods might be possible (Green, White, et al., 2009; Pelletier et al., 2007).

Dynamic body acceleration is measured via tri-axial accelerometers, which can be incorporated into existing biologging devices that are typically externally attached and thus require no additional effort or invasive protocols to deploy. DBA is the sum of the dynamic acceleration along three axes of the body (Wilson et al., 2006; Yoda et al., 2001). Acceleration is achieved through mechanical work performed by muscles, which should be proportional to the amount of energy being used to move (Gleiss et al., 2011; Halsey, Shepard, et al., 2011). As such, DBA does not provide information on fluctuations in resting metabolic rate, unless these changes are accompanied by some form of acceleration (e.g. shivering; Green, Boyd, et al., 2009; Hicks et al., 2017; Wilson et al., 2019). Further, the efficiency with which mechanical work can be fuelled by chemical energy can differ depending on the mode of locomotion, thus behaviour-specific calibrations are likely needed (Gómez Laich et al., 2011; Halsey, White, et al., 2011). Accelerometers can also detect environmental acceleration (e.g. from wind or waves), which may bias energy estimates during passive forms of locomotion (e.g. soaring flight) or in certain environments (e.g. waves while floating).

In addition to being applied as a measure for fine-scale changes in energy expenditure, DBA has been demonstrated to

be a good predictor of DEE (e.g. Elliott et al., 2013; Jeanniard-du-Dot et al., 2017; Stothart et al., 2016). These validation studies, comparing average DBA to field metabolic rates determined using doubly labelled water, typically conclude that behaviour-specific DBA calibrations significantly improve the accuracy of estimating DEE in species that use a range of locomotory modes. Instead of calculating DBA, acceleration patterns can also be used to identify different behaviours (e.g. locomotory modes), allowing for detailed partitioning of time between activities. A constant energetic cost can then be assigned to each behaviour, either measured in captivity or based on biomechanical models or allometric relationships, which can be integrated in time to estimate DEE (i.e. a TEB). The TEB approach thus ignores changes in energetic costs within a behaviour caused by, for example, changes in speed or body mass (Pennycuik, 2008), though circumvents the need for calibration relationships to interpret DBA.

The use of accelerometers is rapidly gaining popularity as an alternative method for measuring energy expenditure in free-ranging animals (Brown et al., 2013; Joo et al., 2020). However, while DBA has been successfully validated across a range of taxa for walking (Halsey et al., 2009; Wilson et al., 2006), the relationship between DBA and energy expenditure during other modes of locomotion has been less extensively explored, particularly for flapping and soaring flight (Hicks et al., 2017). Heart rate, having equally high temporal resolution and potential to record over extended time-scales as accelerometers, presents a good standard against which we can assess the effectiveness of using acceleration as a proxy for energy expenditure on both fine and daily scales (Hicks et al., 2017).

In this study, we concurrently measure acceleration and f_h on free-ranging lesser black-backed gulls *Larus fuscus*, a seabird species that uses a range of locomotory behaviours (flapping flight, soaring flight and walking), and rests on both land and water. Our first objective is to examine how DBA corresponds to energy expenditure when measuring both across and within different behaviour modes in a wild setting, by comparing it to the f_h method. This includes two parts: (1a) We compare the relative changes within both proxies among different behaviour modes (flapping, soaring, walking, floating and resting on land). Here, both soaring flight (being a passive vs powered locomotory mode) and floating (being susceptible to environmental variation) are of particular interest as DBA may be less able to predict metabolic rate of these behaviours. We report average energetic costs of these behaviour modes, which can be used in TEB analyses. (1b) We examine the relationships between DBA and metabolic rate estimated from f_h , both separately within a behaviour, as well as across bouts of all behaviours. Our second objective is to determine how acceleration data can best be used to estimate DEE. To do so, we compared DEE from DBA and TEB methods to that from the f_h method, using the average costs per behaviour and relationships between DBA and metabolic rate found in objective 1. Finally, we explore how variation in resting metabolic rate, based on daily minimum

f_h , influences the relationship between f_h -based and acceleration-based estimates of DEE.

2 | MATERIALS AND METHODS

2.1 | Capture, tagging and implantation

Four male and two female lesser black-backed gulls were captured during incubation using a walk-in trap between 28 and 31 May 2019 in their breeding colony (Texel, the Netherlands, 53°00'N, 04°43'E). The birds were colour-ringed and measured, and solar-powered GPS trackers with tri-axial accelerometers (13.5 g, 5CDLe trackers, UvA Bird tracking system; Bouten et al., 2013) were attached to the back of the birds using a Teflon ribbon 'wing harness' (Thaxter et al., 2014). This GPS tagging method does not appear to impact breeding productivity (Kavelaars et al., 2018) or colony return rates (Thaxter et al., 2016), though nest desertion occasionally occurs after capture and handling of both tagged and untagged birds. Heart rate (f_h) was derived from electrocardiograms measured with implantable loggers (15 g, size M Stellar implants, TSE systems, www.tse-systems.com). Heart rate loggers were surgically inserted in the field under full anaesthesia immediately following ringing and GPS attachment (see Appendix S1 for implantation methods). The combined weight of the GPS trackers and heart rate loggers was 3.2%–4.6% of body mass.

GPS fixes, including location, altitude, instantaneous speed and direction, were recorded every 15 min within the colony and every 5 min outside the colony. Acceleration was recorded in 1-s segments at 20 Hz every 2.5 min as well as directly following each GPS fix. An electrocardiogram (ECG) was recorded for a 4-s interval at 500 Hz, with 82% of the data being collected at a 5-min interval, and the remainder at a 10-min interval. Because we used separate systems, acceleration and ECG measurements could not be exactly synchronised. Base stations in the colony were used to remotely program recording schedules and download data for both GPS and f_h systems. Long data gaps sometimes occurred in f_h data as a result of breaking contact during download.

Five birds resumed incubation following release. The sixth bird abandoned its nest and only GPS and acceleration data, but no f_h data could be recovered due to different transmission ranges. Data were collected from the remaining individuals over a period of 3–5 weeks while they were returning regularly to the colony to incubate or provision chicks. Air temperatures during this period ranged between 11.1 and 32.7°C, within the thermal neutral zone for this species (Appendix S2), and sea surface temperatures ranged between 12.3 and 18.6°C (ERA5; Hersbach et al., 2018).

All six birds returned to the colony in 2020, demonstrating birds can successfully migrate and survive with these devices long term. As captured individuals will not re-enter traps during the same breeding season, we have been trying to recapture individuals during subsequent breeding seasons to remove both devices. Currently, three

TABLE 1 Number and median and maximum durations (dur.) of behavioural bouts, along with mean (\pm standard deviation) heart rates (f_h), DBA and metabolic rate estimate from f_h (MR_{hr}) and DBA (MR_{DBA}), per behaviour. Ratio to resting metabolic rate was based on MR_{hr} and the resting metabolic rate measured in the lab ($RMR_{lab} = 4.59$ W)

Behaviour	No. bouts	Med. dur. (min)	Max. dur. (min)	Mean. f_h (beats/min)	Mean. DBA (g)	MR_{hr} (W)	MR_{DBA} (W)	$MR_{hr}:RMR_{lab}$
Flap	290	15	119	360 ± 60	0.661 ± 0.052	32.0 ± 11.1	19.0 ± 1.2	7.0
Walking	75	12	49	200 ± 37	0.199 ± 0.036	8.5 ± 3.2	8.2 ± 0.8	1.8
Soar	68	11	88	181 ± 37	0.123 ± 0.038	7.9 ± 3.8	6.4 ± 0.9	1.7
Float	201	15	100	162 ± 44	0.121 ± 0.030	6.6 ± 3.8	6.4 ± 0.7	1.4
Rest	1,108	27	396	160 ± 42	0.028 ± 0.021	6.2 ± 3.4	4.2 ± 0.5	1.3

birds have been successfully recaptured and released following sensor removal.

2.2 | Energy expenditure

Vectorial dynamic body acceleration (DBA) was calculated as in Wilson et al. (2019), and f_h was extracted from ECG (full methodology in Appendix S3). A calibration for DBA was calculated by walking two captive lesser black-backed gulls on the treadmill and used to estimate metabolic rate from DBA (see Appendix S4 for full methods on estimating energy expenditure in this study, and Appendix S2 for full methods and results of captive work). Heart rate was converted to metabolic rates using an allometric calibration equation (Bishop & Spivey, 2013), the fit of which was confirmed using metabolic measurements of lesser black-backed gulls in captivity and expected values based on published literature (Appendix S5 and Figure S1).

As f_h and DBA measurements could not be exactly synchronised in time (see Section 2.1), we identified bouts from periods where consecutive accelerometer measurements were classified as the same behaviour (flapping, soaring, walking floating and resting) and averaged DBA, f_h and energy estimated from each proxy over the bout (Appendix S4).

2.3 | Data analysis

Linear models (LMs) were the primary statistical test used to compare among proxies. Typically mixed models are employed to control for individual effects; however, due to the low number of individuals, estimates of individual random effects were sometimes singular. Instead, individual was included as a fixed effect, and the data were centred over the individual factor so the model intercept falls at the group centre (Schielzeth, 2010). For LMs without convergence issues, Akaike's information criterion (AIC; Burnham & Anderson, 2010) usually indicated that it was more parsimonious to include individual as a fixed factor than a random effect, so we use fixed factors throughout for consistency. Instead of reporting parameters estimated for all levels of the individual factor, we report standard deviation around the mean of the individual intercepts. To account for potential effects of post-surgical recovery on f_h , the four

days following surgery were excluded from analyses. All analyses were performed in R version 4.0.2.

2.3.1 | Objective 1a. Comparison of DBA to heart rate: Relative changes among behaviours

To compare the relative changes in DBA and f_h , metabolic rate estimated from heart rate (MR_{hr}) and metabolic rate estimated from DBA (MR_{DBA}) among bouts of flapping, soaring, walking, floating and resting, the proxies and estimated MRs were used as the response variable in a LM with behaviour and individual as fixed factors. Significant differences between behaviours within a given proxy were assessed for each method using Tukey's post hoc test. Comparisons among proxies were not tested as DBA and f_h did not have the same units, while differences in MR_{hr} and MR_{DBA} were not tested as the walking calibration for DBA was not expected to be applicable to other behaviours.

2.3.2 | Objective 1b. Comparison of DBA to heart rate: Linear relationships

MR_{hr} of behavioural bouts was modelled as a linear function of DBA, behaviour mode and their interaction, using LMs with individual as a fixed factor, to assess whether the relationship between DBA and energy expenditure changes across behaviours. AIC was used to assess the most parsimonious groupings of behaviours (i.e. whether some or all behaviours demonstrate the same DBA- MR_{hr} relationship). To examine the relationship within a behavioural mode, we used separate LMs of MR_{hr} as a function of DBA per behaviour, including individual as a factor.

2.3.3 | Objective 2. Using acceleration to estimate DEE

To examine how acceleration can best be used to estimate DEE, we averaged MR_{hr} over the course of a day (Portugal et al., 2016), weighted by the interval between f_h measurements, to obtain an average field metabolic rate, then multiplied by a 24-hr period (DEE_{hr}). We then estimated DEE from four acceleration-based methods. Method

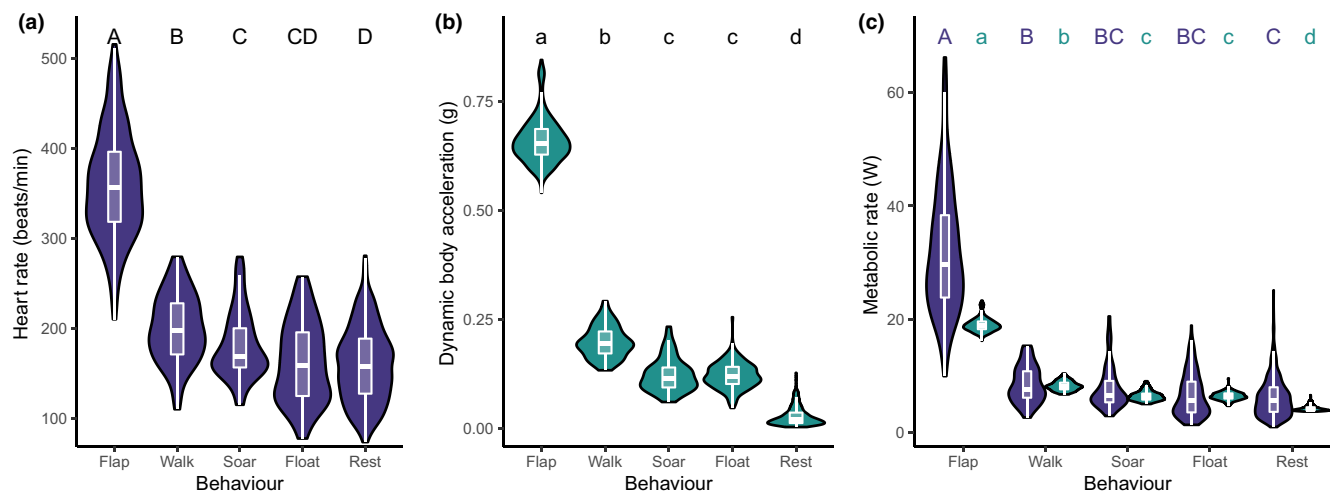


FIGURE 1 Violin and boxplots of (a) heart rate, (b) DBA and (c) metabolic rate estimated from each proxy (heart rate in purple and DBA in teal) for different behavioural modes ($n = 1,742$ bouts). Violin plots outline kernel probability densities and boxplots show median and inter-quartile range (IQR) with whiskers denoting $1.5 \times$ IQR. Significant differences based on Tukey's tests per proxy are indicated above boxplots, where behaviours with the same letter are not significantly different ($p > 0.05$). In (c), differences between proxies were not tested, indicated by letter case

1 converts DBA to MR using a single calibration relationship across all behaviours ($\text{DBA}_{\text{single}}$) and method 2 uses behaviour-specific calibrations to convert DBA to MR ($\text{DBA}_{\text{behave}}$). The LMs calculated in Section 2.3.2 were used for these conversions. Method 3 estimates DEE using a TEB differentiating five behaviour modes ($\text{TEB}_{\text{behave}}$), and method 4 uses a simplified TEB only differentiating flight, floating and resting, such as can typically be reconstructed from GPS data (TEB_{GPS}). The mean MR_{hr} for each behaviour calculated in Section 2.3.1 and reported in Table 1 were used in $\text{TEB}_{\text{behave}}$. For TEB_{GPS} , a single cost of flight was estimated from the mean of MR_{hr} while flapping and soaring, weighted by the flap-soar ratio over the study (65.9% flapping). Walking was combined with resting and assigned the mean MR_{hr} while resting. Unclassified accelerometer measurements were excluded. Acceleration-based estimates of MR were averaged over the day and weighted by the time until the next acceleration measurement and multiplied by a 24-hr period. In case of a data gap, only periods when both proxies had data were used in daily averages. Days with less than 12 hr of coverage were discarded.

As both measurement methods contain error, we used major axis regression to examine the relationship between each accelerometry method and DEE_{hr} . To account for uncertainty in the conversion of acceleration to metabolic rate, we used a bootstrapping approach. First, 500 potential calibration parameters (slope and intercepts) or behaviour costs (depending on the acceleration metric) were simulated using a normal distribution centred at the parameter mean and with a standard deviation equal to the standard error around the parameter mean. These simulated calibration relationships and behaviour costs were then used to convert acceleration to metabolic rate and estimate DEE, resulting in 500 sets of estimated DEE per acceleration metric. Next, to estimate standard error around the regressions, each DEE set was bootstrapped 500 times resulting in a total of 250,000 resampled datasets. The 2.5% and 97.5% quantiles of the slopes and intercept of

the major axis regressions on these resampled datasets were used as 95% confidence intervals.

We also explored how daily minimum f_h (as an indicator of variation in resting metabolic rate), calculated as the mean of the lowest three consecutive f_h measurements per day, influenced DEE_{hr} , the acceleration-based estimates of DEE and their relationship.

Ethical approval for work with animals was approved by the Centrale Commissie Dierproeven under licence number AVD8020020174225, following the Dutch Animal Welfare Act Articles 9, 10 and 11 of animal experiment documents. Access to the colony was granted by the Staatsbosbeheer and Regionale Uitvoeringdienst Noord-Holland Noord (RUD.241638).

3 | RESULTS

We collected a total of 1,285 hr of concurrent heart rate-accelerometer data. A summary of the individuals, number of bouts per individual and their resting and flapping heart rates is given in Table S1.

Resting was the most common activity exhibited (63.3% of accelerometer measurements). Floating accounted for 8.7% of measurements, resulting in 71.9% of measurements being taken while inactive. Flapping flight was the most common form of locomotion (12.8% of measurements), followed by soaring (5.8%), walking (5.6%) and mixed flight (1.4%), with 2.4% of segments being unclassified.

3.1 | Objective 1a. Comparison of DBA to heart rate: Relative changes among behaviours

A total of 1,742 behaviour bouts were retained in the analysis. During flapping flight, f_h was significantly higher compared to other

behaviours (Tukey's test: $p < 0.001$ for all comparisons, Figure 1a). Heart rates for the remaining behaviours were more similar and overlapping. Walking had the next highest f_h , followed by soaring, while floating and resting had similar f_h ranges. Heart rate while floating was statistically indistinguishable from soaring ($p = 0.17$) and resting ($p = 0.48$), but the other behaviours were significantly different ($p < 0.02$). After converting to MR_{hr} , walking remained significantly different from resting ($p < 0.001$), though not from soaring or floating ($p = 0.61$ and $p = 0.14$), and soaring and floating were not statistically different from resting ($p = 0.23$ and $p = 0.12$; Figure 1c).

Changes in DBA (and MR_{DBA}) followed a similar pattern to f_h though with less overlap between behaviours: flapping was noticeably higher than all other behaviours, followed by walking, then soaring and resting being lowest (all significantly different with $p < 0.001$, Figure 1b). However, unlike f_h , DBA while floating was significantly higher than resting (t test: $p < 0.001$), instead being similar to DBA during soaring ($p = 0.89$).

The mean f_h , DBA and metabolic rates of each behaviour mode, along with the ratio between MR_{hr} and resting metabolic rate measured in captivity ($RMR_{lab} = 4.59$ W, Appendix S2) are reported in Table 1. Mass-specific metabolic rates are reported in Table S2. Applying the DBA calibration derived while walking to other behaviours severely underestimated the costs of flapping flight compared to MR_{hr} (Figure 1c), and mean values while soaring and resting were also underestimated (differences of 1.5 and 2 W respectively). The lab-derived DBA calibration and MR_{DBA} behaviour estimates are not used further for any behaviours in this study.

3.2 | Objective 1b. Comparison of DBA to heart rate: Linear relationships

After reclassifying mixed flight as flapping or soaring (Appendix S4), we had 1,772 behaviour bouts. The top LM for predicting MR_{hr} based on AIC includes an interaction between behaviour and DBA, indicating that the relationship between DBA and MR_{hr} changes depending on the behavioural mode (Table 2). Grouping behavioural classes did not increase parsimony, with the top-ranked model including all five behavioural modes (Table S3). DBA without any behaviour-specific adjustments was positively correlated with MR_{hr} ($r^2 = 0.743$, expected given similarity in relative changes among behaviours, Figure 1), though this was the lowest performing model.

TABLE 2 AIC comparison and r^2 values of linear models of MR_{hr} by DBA and behaviour, with all five behavioural classifications used. All models include individual as a fixed factor

Model	df	Δ AIC	r^2
$MR_{hr} \sim DBA + Behaviour + DBA \times Behaviour + ID$	15	0.00	0.766
$MR_{hr} \sim DBA + Behaviour + ID$	11	14.27	0.763
$MR_{hr} \sim Behaviour + ID$	10	40.70	0.759
$MR_{hr} \sim DBA + ID$	7	145.57	0.743

The model including just behaviour classification explained slightly more variation in MR_{hr} than that with only DBA, suggesting DBA did not improve upon using a single cost per behaviour (Table 2). Moreover, when the MR_{hr} -DBA relationship was considered separately for each behaviour, MR_{hr} and DBA were poorly correlated for most behaviours (Figure 2, Table S4). Only resting had a significant positive relationship between MR_{hr} and DBA, while other behavioural modes had no significant relationship (Figure 2). Plots of MR_{hr} versus DBA per behaviour along with confidence intervals and individual intercepts are shown in Figure S2 and results of LMs are reported in Table S4.

3.3 | Objective 2. Using acceleration to estimate DEE

Sixty-nine bird-days had coverage from both proxies for more than 12 hr. DEE estimated by any acceleration method increased with DEE_{hr} . DBA_{single} consistently overestimated DEE relative to DEE_{hr} (Figure 3a, Table 3). The other three models, DBA_{behave} , TEB_{behave} and TEB_{GPS} resulted in similar DEE estimates (Figure 3a). Slopes of these models fell between 0.55 and 0.70, underestimating DEE on days with high DEE_{hr} and overestimating on days with low DEE_{hr} . The TEB_{GPS} model explained less variation in DEE_{hr} than the other acceleration methods (i.e. lower r^2 , Table 3). Confidence intervals around DBA_{behave} were wide due to uncertainty around the behaviour-specific calibrations (Figure 3b). These confidence intervals include the 1:1 relationship with DEE_{hr} , so this method has potential to predict DEEs closer to predictions from DEE_{hr} if better calibrations can be obtained.

To understand why the acceleration methods had slopes shallower than a 1:1 relationship with DEE_{hr} , we explored the influence of daily minimum f_h on our DEE estimates. Minimum f_h was positively correlated with DEE_{hr} ($r = 0.29$), but not with the acceleration estimates ($-0.18 < r < -0.05$ for all methods). As such, days with high minimum f_h tend to be days with high DEE_{hr} , and days with high minimum f_h tend to fall below the line of equality (i.e. underestimated by acceleration) and vice versa (see Figure 3b-d for an example using DBA_{behave} , for other acceleration methods see Figure S3). Thus, the limited ability of acceleration methods to detect variation in resting metabolic rates partially explains why the slope of the relationship between DEE_{hr} and DEE estimated from acceleration is shallower than the line of equality.

4 | DISCUSSION

While the use of DBA as an estimate of metabolic rate in free-ranging animals is becoming increasingly popular (Brown et al., 2013; Joo et al., 2020), few studies have investigated how well it functions across multiple behaviour modes in the wild, particularly at high temporal resolutions (Hicks et al., 2017) and in a species that uses passive modes of locomotion such as soaring flight (Duriez et al., 2014).

FIGURE 2 MR_{hr} versus DBA of behavioural bouts ($n = 1,772$). Centred intercept and slope of linear models per behaviour are represented by coloured lines and across all bouts by the dashed black line ($p < 0.001$, $r^2 = 0.743$). Model parameters and statistics are reported in Table S4

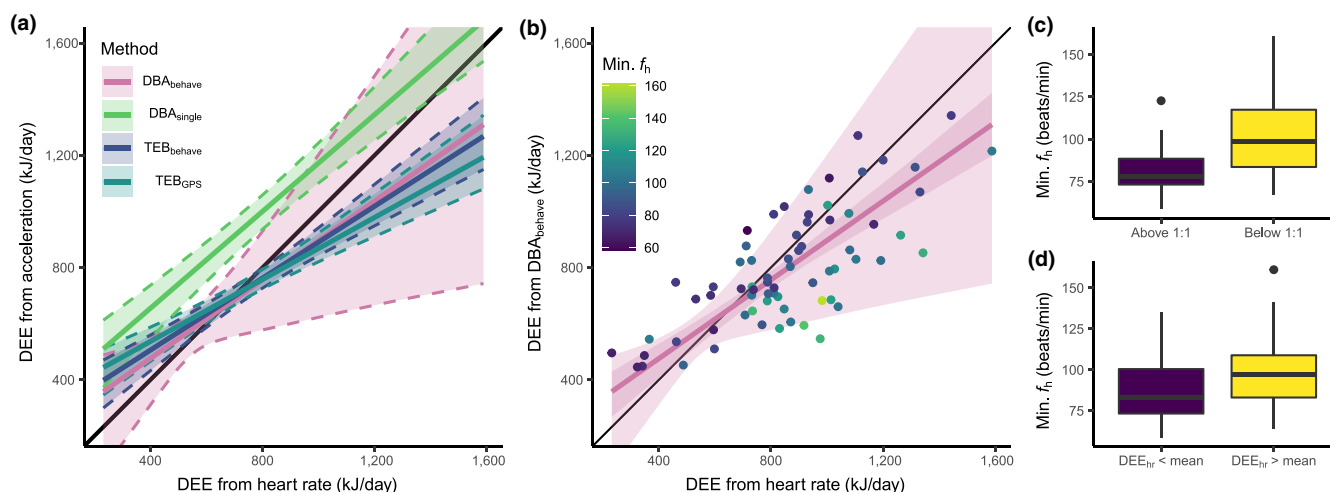
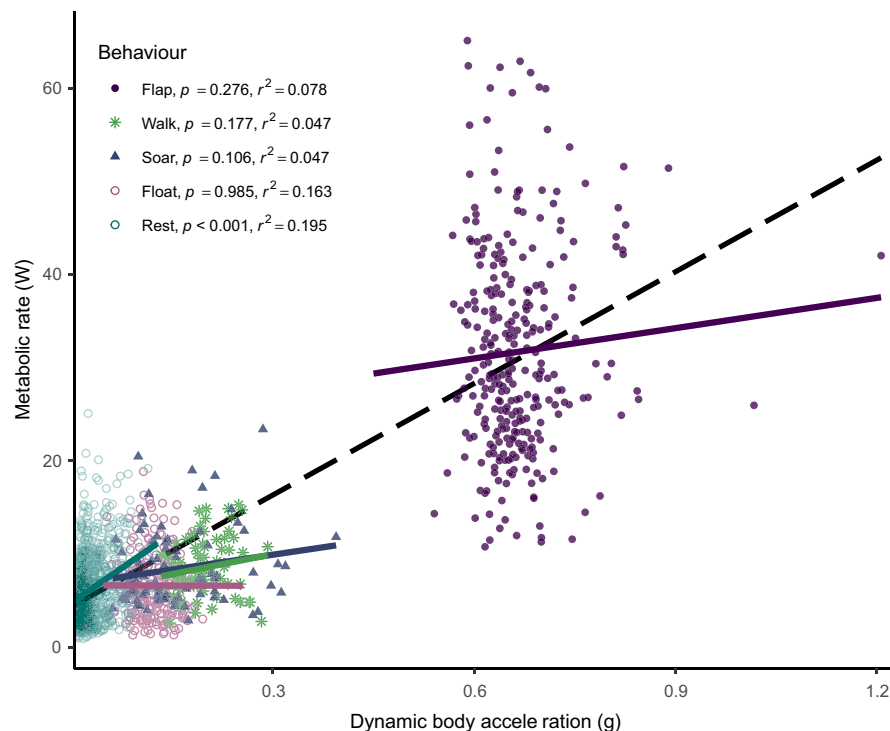


FIGURE 3 (a) Major axis regressions of acceleration-based estimates of daily energy expenditure (DEE) versus estimates from heart rate (DEE_{hr}). Methods include DBA converted to MR with a single relationship across all behaviours (DBA_{single}), DBA converted with behaviour-specific calibrations (DBA_{behave}), a five-behaviour time-energy budget (TEB_{behave}) and a simplified time-energy budget that could be derived from only GPS (TEB_{GPS}). Acceleration methods are distinguished by colour. 95% confidence intervals including uncertainty in conversion from acceleration to metabolic rate are identified by the shaded regions with dashed lines. The line of equality is shown with a black line. (b) A scatter plot showing the relationship between DEE estimated DBA_{behave} versus DEE_{hr} . Points are coloured by daily minimum heart rate ($min. f_h$). Major axis regression line is shown in pink with 95% confidence intervals shown by the shaded areas, where the darker shaded region shows the confidence interval around the regression before accounting for uncertainty in converting acceleration to metabolic rate, and the lighter area shows the confidence interval based on our bootstrapping approach. The line of equality is shown in black. (c) Boxplots showing distribution of $min. f_h$ on days in panel (b) that fall above and below the line of equality. (d) Boxplots showing distribution of $min. f_h$ on days where DEE_{hr} is below or above the mean DEE_{hr} (858 kJ/day). Scatter plots as shown in (b) for the other three methods can be found in Figure S3

In this study, we measured DBA alongside f_h in five free-ranging lesser black-backed gulls. We found DBA generally suggested similar relative differences between behaviours as the f_h method, except during floating, which was overestimated by DBA. DBA was thus positively correlated with MR_{hr} when all behaviours are considered

together. Our results demonstrate that the relationship between MR_{hr} and DBA changes between behaviour modes, though variation between these proxies within a behaviour mode was high and behaviour-specific relationships were not statistically significant. At a daily scale, DBA performed comparably to TEBs for predicting

TABLE 3 Summary of major axis regression models of daily energy expenditure estimated from acceleration-based methods (DBA and time-energy budgets) versus estimated from heart rate. DBA_{single} is DBA calibrated with a single relationship across all behaviours, DBA_{behave} is calibrated with behaviour-specific relationships, TEB_{behave} is a five-behaviour time-energy budget and TEB_{GPS} is a simplified time-energy budget that could be reconstructed using only GPS data. 95% confidence intervals result from our bootstrapping approach, accounting for uncertainty in calibrations and behaviour costs used to convert acceleration to metabolic rate

Model	Intercept (95% CI)	Slope (95% CI)	Model r^2
DBA _{single}	310 (129–444)	0.86 (0.70–1.07)	0.54
DBA _{behave}	195 (–251–432)	0.70 (0.20–1.43)	0.56
TEB _{behave}	249 (114–350)	0.64 (0.51–0.81)	0.54
TEB _{GPS}	316 (179–410)	0.55 (0.43–0.73)	0.45

DEE, though neither approach had a 1:1 relationship with f_h -based estimates. This was at least partially due to undetected fluctuations in resting metabolic rates by acceleration-based methods.

4.1 | Comparison of DBA to heart rate

While accelerometry provides great potential for measuring energy invested into physical activity in the wild, many studies overlook the crucial step of determining the relationship between DBA and energy expenditure (Halsey & Bryce, 2021). This is particularly important for systems where a range of behaviour modes and habitats are utilised, as variation in muscle efficiency and environmental noise may result in deviations from a single linear fit (Gómez Laich et al., 2011). In our study, the relative changes in both proxies among behaviour modes were generally similar, with the exception of floating which was overestimated by DBA. When DBA was converted to metabolic rate by extrapolating a linear calibration derived only while walking (MR_{DBA}), only the average metabolic rate while walking corresponded with the average costs estimated from heart rate (MR_{hr}). This suggests the relationship between DBA and energy expenditure changes among behaviour modes, thus behaviour-specific calibration will be required in species that move using different locomotory modes.

We were particularly interested in whether DBA would properly represent energy expenditure while soaring. During soaring flight, animals capture rising air with wings held out isometrically, manoeuvring using small adjustments to wing and tail position (Gillies et al., 2011). As isometric muscle contractions do not result in acceleration, DBA cannot detect all the work done by the animal (Gleiss et al., 2011). Instead, much of the measured acceleration is likely resulting from air turbulence. However, DBA and f_h both showed similar relative differences between soaring and other behaviours, falling between walking and resting. This suggests that environmental acceleration is similar to energy required to statically control

wing position, though this may be subject to deviations under different soaring styles (e.g. orographic, thermal and dynamic soaring). Two other studies that record DBA and f_h simultaneously in obligate soaring birds also found a good relationship between DBA and f_h during flight (Duriez et al., 2014; Weimerskirch et al., 2016).

In contrast, we found that DBA during floating was higher than at rest on land, whereas f_h was not significantly different between floating and resting. Higher DBA is presumably due to added acceleration from waves. When environmental acceleration may influence DBA estimates, calibrating DBA in the environment which it is being used could partially correct this bias, for instance we found floating has a higher intercept than resting on land. However, this cannot account for spatial or temporal variation in environmental conditions, such as differences in wave action across various bodies of water and weather conditions. From a physiological standpoint, it is interesting that we found no significant difference between f_h on land and on water. Metabolic rates of diving and floating animals are often elevated because water has higher thermal conductance and a greater specific heat capacity than air, requiring more energy to maintain body temperature (Bevan et al., 1995; Humphreys et al., 2007). Our results suggest that there is no increased thermoregulatory cost of resting on water at temperatures above 12°C in lesser black-backed gulls.

Corresponding with similar relative changes in both proxies among behaviours, when all behaviour bouts were pooled, we found that DBA was positively correlated with MR_{hr}. However, the top model for predicting MR_{hr} from DBA of behavioural bouts included an interaction term between all five behavioural modes, further indicating that the relationship between MR_{hr} and DBA changes by behaviour at the level of a behavioural bout. In line with our results, previous studies on seabird species have demonstrated that DBA tends to be a robust proxy when comparing across different behaviour modes, either by comparing it to the high resolution f_h method (Hicks et al., 2017) or to the lower resolution doubly labelled water method (Elliott et al., 2013; Stothart et al., 2016), with the general consensus that behaviour-specific calibrations will improve estimation of energy expenditure. These studies focus on species that primarily dive and use flapping flight, while our study now additionally adds an animal that can travel using soaring flight.

When comparing behaviour bouts within a single behaviour mode we did not find significant positive relationships between DBA and MR_{hr}. Due to the imperfect temporal pairing between f_h and DBA, we cannot conclude whether this is because DBA (or f_h) do not properly depict changes in energy expenditure within a behaviour mode, or because gulls adjust their effort on finer temporal resolutions than we could capture with our recording schedules. The latter is highly probable given the fluid flap-soar flight style of gulls. Even considering this we may still expect some average differences in effort between behaviour bouts. For example, gulls commuting over sea flap continuously along direct routes, where effort across the entire flight bout may vary depending on whether the bird is experiencing head-, tail- or crosswinds (McLaren et al., 2016), or with changes in body mass before and after foraging. The average effort

while flapping during a commuting flight may likewise differ from the effort during competitive interactions while foraging behind a fishing vessel or at a refuse site. Hicks et al. (2017), who also continuously recorded and compared DBA to energy expenditure estimated from f_h in wild European shags *Phalacrocorax aristotelis*, found positive relationships within a behaviour for flapping flight and resting, though not diving behaviour. They also had high error around their behaviour regression lines, though demonstrated that much of the error could be accounted for by the uncertainty around the f_h to energy expenditure conversion, rather than necessarily originating from the DBA method.

Differences in body mass both among and within an individual can also influence overall energy expenditure, as well as the relationship between energy expenditure and both f_h and DBA. Work, the mechanical equivalent of energy expenditure, is proportional to the product of body mass and acceleration (Gleiss et al., 2011). Thus, the slope of the relationship between DBA and energy expenditure should increase with body mass (i.e. a heavier mass will show a smaller increase in acceleration for a given increase in energy expenditure compared to a lighter mass; Halsey et al., 2009). As we have a small number of individuals with only a single body mass measurement each, we cannot properly account for the influence of body mass on energetic costs of different behaviours in our study, nor for the influence of within-individual fluctuation in body mass on calibration relationships which may be an additional source of error around those relationships.

Overall, our comparison between DBA and MR_{hr} across behaviour bouts suggests that DBA does perform reasonably well as a proxy for energy expenditure across a range of behaviour modes, including soaring flight. However, DBA overestimated energy expenditure when floating on the water, likely as a result of environmental acceleration from waves. While within a behaviour mode we did not find significant, positive correlations between DBA and MR_{hr} , sources of methodological error may be obscuring our ability to detect these relationships. We encourage more validation studies with either continuous or synchronised recording of these methodologies at high temporal resolutions to determine the degree to which either f_h or DBA can detect fine-scale variation in energy expenditure for various modes of locomotion.

4.2 | Using acceleration to estimate DEE

On a daily scale, TEBs performed comparably for estimating DEE_{hr} as DBA calibrated with behavioural interactions, while the DBA model without activity-specific calibrations consistently overestimated DEE. This is in contrast to validation studies comparing DBA to energy estimated from doubly labelled water in diving seabird species, where DBA predicted total energy expenditure better than TEBs, at least when behaviour-specific slope parameters were estimated (Elliott et al., 2013; Stothart et al., 2016). The slope of the relationship between acceleration-based estimates of DEE and the f_h estimates was shallower than 1, which we demonstrate is at least

partially caused by day-to-day fluctuations in resting rates which are better detected using the heart rate method. Confidence intervals around the relationship between DEE estimated from DBA using behaviour-specific calibrations (DBA_{behav}) and DEE_{hr} were wide and included the line of equality. Wide confidence intervals were largely due to the uncertainty in the behaviour-specific calibration relationships, so this method has potential to predict DEE closer to DEE_{hr} if stronger calibration relationships can be obtained.

A simplified time budget (TEB_{GPS}), where flight mode was pooled, had a similar relationship with DEE_{hr} as the complete TEB, albeit with more error. This was surprising given the large difference in energetic cost between soaring and flapping flight. This suggests that gulls were using a relatively similar flap-to-soar ratio throughout the study. However, when comparing across season or locations, flap-to-soar ratio may become less predictable. For example, Flack et al. (2016) demonstrated that DBA during migration for white storks *Ciconia ciconia* migrating south of the Sahara was lower than those north of the Sahara, corresponding to increased thermal uplift facilitating soaring at lower latitudes.

Metabolic rates estimated from DBA without a behaviour-specific calibration fell furthest from the line of equality, though its slope was similar and even slightly closer to a slope of 1 than the other methods. We caution that our finding may not be extrapolated to all systems. For example, Jeanniard-du-Dot et al. (2017) found DBA did not correlate with DEE in foraging fur seals unless behaviour-specific relationships were applied.

The variation explained by all models at the daily level ($r^2 = 0.48$ – 0.56) was lower than those reported in doubly labelled water studies (Elliott et al., 2013; Stothart et al., 2016). We demonstrated that some of this error was likely related to variation in resting metabolic rates which can result from thermoregulation, digestion and production costs, though thermoregulatory costs are expected to have been constant throughout this study. Error caused by undetected variation in resting metabolic rates when using acceleration-based methods will be more significant in a bird with low versus high activity levels. The gulls in this study spent on average 72% of the day in inactive behaviours (resting or floating) and thus DBA may not perform as well in our system compared to animals with higher activity levels. Additionally, while recording over a longer time period should smooth out some of the error arising due to lack of synchrony between our proxy measurements (Green, 2011), using a sampling approach still likely contributes more error compared to continuous measures of DEE that were used in validations with doubly labelled water.

Given that detailed TEBs perform comparably to DBA at estimating DEE, there are situations where TEBs may be preferable: (a) For studies examining how energy is partitioned among behaviours, TEBs can provide a clear link to the underlying cause behind variation in energy expenditure between individuals, habitats or strategies (Sage et al., 2019). (b) For studies where the accelerometer is not located near the centre of mass (e.g. neck collars, mounted to tail feathers), DBA accuracy may be decreased (Wilson et al., 2019). Additionally, the TEB method can be used to compare energy

expenditure across systems where different attachment methods have been used (Garde et al., 2021). (c) For species using activities which may be unduly influenced by environmental acceleration (e.g. floating).

DBA, however, is advantageous because it does not require categorising behaviour into discrete categories, leading to unknown or intermediate behaviours being discarded from TEBs. Also, if DBA is used without classifying behavioural modes, which typically requires raw acceleration profiles, it can be calculated on the tracker, reducing the amount of data collected per bout and thus permitting more frequent or longer recording periods (Nuijten et al., 2020). Note, however, that this would preclude the use of behaviour-specific calibration equations. For studies spanning seasons or years, where body mass of animals may fluctuate systematically causing changes in activity costs, DBA should detect some of the resulting change in effort. Finally, the accuracy of the TEB approach depends on reliable estimates of the costs of various locomotory modes for the species of interest (Elliott, 2016), which may not be available for all species.

None of the accelerometry-based methods fully accounted for variation in resting metabolic rates, as can be captured using the f_h method. This is a drawback of all acceleration-based methods, particularly if the purpose is to quantify an absolute value of energy expenditure. However, while activity may be highly unpredictable, variation in resting costs such as thermoregulation, digestion and production may be more easily modelled and added to activity costs measured via acceleration (Gleiss et al., 2011). Further, for questions relating to behavioural strategies and decision-making, where fluctuations in resting process may be independent of the behaviour being examined, acceleration-based methods are likely still suitable. Preferably, the combined use of f_h and acceleration presents an opportunity to examine changes in both activity and resting costs throughout the year and across diverse environmental conditions (Bishop et al., 2015; Grémillet et al., 2005).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.M.B., J.S.-B. and W.B. conceived and led the study; K.C.J.C. helped design and facilitated data collection in the field; B.A.N. facilitated data collection in captivity and advised on data analysis; J.M.B. analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R code are available on Zenodo <https://doi.org/10.5281/zenodo.6424631> (Brown et al., 2022).

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