Acceleration as a proxy for energy expenditure in a facultative-soaring bird

Comparing dynamic body acceleration and time-energy budgets to heart rate

Brown, J.M.; Bouten, W.; Camphuysen, K.C.J.; Nolet, B.A.; Shamoun-Baranes, J.

DOI
10.1111/1365-2435.14055

Publication date
2022

Document Version
Final published version

Published in
Functional Ecology

License
CC BY

Citation for published version (APA):
Acceleration as a proxy for energy expenditure in a facultative-soaring bird: Comparing dynamic body acceleration and time-energy budgets to heart rate

J. Morgan Brown1 | Willem Bouten1 | Kees C. J. Camphuysen2 | Bart A. Nolet1,3 | Judy Shamoun-Baranes1

1Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands
2Department of Coastal Systems, NIOZ Royal Institute for Sea Research, Texel, The Netherlands
3Department of Animal Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands

Correspondence
J. Morgan Brown
Email: jbrow247@alumni.uwo.ca

Funding information
Koninklijke Nederlandse Akademie van Wetenschappen, Grant/Award Number: KNAWWF/807/19004; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: PGSD3-503551-2017

Handling Editor: Steven Portugal

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
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 andlogistically challenging in field conditions. The $f_h$ method relies on Fick’s equation, which states that the rate of oxygen consumption ($V_{O_2}$) 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 $V_{O_2}$ 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 (Pennycuick, 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 heart rate 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 heart rate 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 heart rate, 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 heart rate 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 heart rate $f_{hr}$, influences the relationship between $f_{hr}$-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, SCDLe 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 ($f_{hr}$) 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 ECG systems. Long data gaps sometimes occurred in heart rate data as a result of breaking contact during downloading.

Five birds resumed incubation following release. The sixth bird abandoned its nest and only GPS and acceleration data, but no heart rate 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
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 \( f_p \) 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 \( f_p \) 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, \( f_p \), 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 center (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 \( f_p \), 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 \( f_p \) metabolic rate estimated from heart rate (MRhr) and metabolic rate estimated from DBA (MRDBA) 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 \( f_p \) and DBA did not have the same units, while differences in MRhr and MRDBA 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

MRhr 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–MRhr relationship). To examine the relationship within a behavioural mode, we used separate LMs of MRhr 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, as MRhr over the course of a day (Portugal et al., 2016), weighted by the interval between \( f_p \) measurements, to obtain an average field metabolic rate, then multiplied by a 24-hr period (DEEhr). We then estimated DEE from four acceleration-based methods. Method
As both measurement methods contain error, we used major axis regression to examine the relationship between each accelerometer method and DEE$_{hr}$. To account for uncertainty in the conversion of accelerometer 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 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 Uitvoeringsdienst 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, 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 \( f_B \), followed by soaring, while floating and resting had similar \( f_B \) 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 \( MR_{\text{hr}} \), 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 \( MR_{\text{DBA}} \)) followed a similar pattern to \( f_B \) 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 \( f_B \), DBA while floating was significantly higher than other behaviours, following walking, then soaring and resting being lowest (all significantly different with \( p < 0.001 \), Figure 1b).

The mean \( f_B \) and metabolic rates of each behaviour mode, along with the ratio between \( MR_{\text{hr}} \) and resting metabolic rate measured in captivity (\( MR_{\text{hr}} = 4.59 \text{ W} \), 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 \( MR_{\text{hr}} \) (Figure 1c), and mean values while soaring and resting were also underestimated (differences of 1.5 and 2 \text{ W} respectively). The lab-derived DBA calibration and \( MR_{\text{DBA}} \) 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 \( MR_{\text{hr}} \) based on AIC includes an interaction between behaviour and DBA, indicating that the relationship between DBA and \( MR_{\text{hr}} \) 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 \( MR_{\text{hr}} \) (\( r^2 = 0.743 \), expected given similarity in relative changes among behaviours, Figure 1c), though this was the lowest performing model.

The model including just behaviour classification explained slightly more variation in \( MR_{\text{hr}} \) than that with only DBA, suggesting DBA did not improve upon using a single cost per behaviour (Table 2). Moreover, when the \( MR_{\text{hr}} \)-DBA relationship was considered separately for each behaviour, \( MR_{\text{hr}} \) and DBA were poorly correlated for most behaviours (Figure 2, Table S4). Only resting had a significant positive relationship between \( MR_{\text{hr}} \) and DBA, while other behavioural modes had no significant relationship (Figure 2). Plots of \( MR_{\text{hr}} \) 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 \( DEE_{\text{hr}} \)-DBA single consistently overestimated DEE relative to \( DEE_{\text{hr}} \) (Figure 3a, Table 3). The other three models, \( DBA_{\text{behave}}, TEB_{\text{behave}} \) and \( TEB_{\text{GPS}} \) resulted in similar DEE estimates (Figure 3a). Slopes of these models fell between 0.55 and 0.70, underestimating DEE on days with high \( DEE_{\text{hr}} \) and overestimating on days with low \( DEE_{\text{hr}} \). The \( TEB_{\text{GPS}} \) model explained less variation in \( DEE_{\text{hr}} \) than the other acceleration methods (i.e. lower \( r^2 \); Table 3). Confidence intervals around \( DBA_{\text{behave}} \) were wide due to uncertainty around the behaviour-specific calibrations (Figure 3b). These confidence intervals include the 1:1 relationship with \( DEE_{\text{hr}} \), so this method has potential to predict DEEs closer to predictions from \( DEE_{\text{hr}} \) if better calibrations can be obtained.

To understand why the acceleration methods had slopes shallower than a 1:1 relationship with \( DEE_{\text{hr}} \), we explored the influence of daily minimum \( f_B \) on our DEE estimates. Minimum \( f_B \) was positively correlated with \( DEE_{\text{hr}} \) (\( r = 0.29 \)), but not with the acceleration estimates (\( -0.18 < r < -0.05 \) for all methods). As such, days with high minimum \( f_B \) tended to be days with high \( DEE_{\text{hr}} \) and days with high minimum \( f_B \) tend to fall below the line of equality (i.e. underestimated by acceleration) and vice versa (see Figure 3b–d for an example using \( DBA_{\text{behave}} \) 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 \( DEE_{\text{hr}} \) 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).
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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept (95% CI)</th>
<th>Slope (95% CI)</th>
<th>Model $r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBA_single</td>
<td>310 (129–444)</td>
<td>0.86 (0.70–1.07)</td>
<td>0.54</td>
</tr>
<tr>
<td>DBA_behave</td>
<td>195 (–251–432)</td>
<td>0.70 (0.20–1.43)</td>
<td>0.56</td>
</tr>
<tr>
<td>TEB_behave</td>
<td>249 (114–350)</td>
<td>0.64 (0.51–0.81)</td>
<td>0.54</td>
</tr>
<tr>
<td>TEB_GPS</td>
<td>316 (179–410)</td>
<td>0.55 (0.43–0.73)</td>
<td>0.45</td>
</tr>
</tbody>
</table>

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 ($MR_{fh}$). 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 thermo-regulatory 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 $MR_{fh}$. However, the top model for predicting $MR_{fh}$ from DBA of behavioural bouts included an interaction term between all five behavioural modes, further indicating that the relationship between $MR_{fh}$ 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 $MR_{fh}$. 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$_{behave}$) 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$_{grp}$), 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 accelerometer-based methods fully accounted for variation in resting metabolic rates, as can be captured using the $f_{an}$ 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 $f_{an}$ 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).

ACKNOWLEDGEMENTS
The authors thank David Tijssen for conducting surgical implantations of heart rate loggers. Götz Eichhorn provided advice on respirometry and heart rate implants. Frank Majoor caught the gulls for 2018 trials in captivity. Gerrit Hardeman (UvA) wrote the software used to remotely download heart rate data in the field, and Edwin Baaij helped to set up the communication system in the field. Tom Delahanty (TSE systems) provided advise and modifications to the heart rate implants. Quinten Madari provided advise on processing the ECG signal. Daniel Zúñiga (Max Planck Institute for Ornithology) provided advise on surgical implant protocols in birds. They thank Jonathan Green and two anonymous reviewers for their detailed and constructive feedback on an earlier version of this manuscript. They thank the Staatsbosbeheer for providing access to the colony. J.M.B. was supported by NSERC (PGSD3-503551-2017) and the Ecology Fund of the Royal Netherlands Academy of Arts and Sciences (KNAWWF/807/19004). UvA-BiTS studies are facilitated by infrastructures for e-Ecology, developed with support of NLeSC and LifeWatch and carried out on the Dutch national e-infrastructure with the support of SURF Cooperative.

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).

ORCID
J. Morgan Brown https://orcid.org/0000-0003-0307-1229
Willem Bouten https://orcid.org/0000-0002-5250-8872
Kees C. J. Camphuysen https://orcid.org/0000-0002-3469-9070
Bart A. Nolet https://orcid.org/0000-0002-7437-4879
Judy Shamoun-Baranes https://orcid.org/0000-0002-1652-7646

REFERENCES


SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.