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NOTE

Overinflated behavioural energetics: using dynamic body acceleration to accurately measure behaviour duration and estimate energy expenditure

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ABSTRACT: Data loggers that measure acceleration are regularly used to quantify the behavioural energetics of animals. Calculating dynamic body acceleration (DBA) by smoothing acceleration data using a necessarily long-running mean of e.g. ≥ 1 s (the DBA method) is not appropriate for determining behaviour duration. In fact, the DBA method results in the elongation of behaviour durations (mean \pm 95% CI behaviour duration elongation for scallops [n = 10 animals] and humans [n = 10 free-ranging aquatic biologists]: 508.5 ± 277.2 and 19.3 ± 1.1 %, respectively) and consequently an overestimation of energy expenditure (mean \pm 95% CI activity metabolic rate overestimation: 212.5 ± 48.0 and 6.12 ± 0.34 %, for scallops and humans, respectively; overall metabolic rate overestimation: 91.1 ± 29.9 and 4.18 ± 0.20 %, for scallops and humans, respectively). Behaviour duration elongation is of greatest significance when behaviour durations are short (minimum, mean and maximum single behaviour duration for scallops and humans recorded in this study: 0.12 and 0.37, 0.40 and 8.04, 0.84 and 185.73 s, respectively). Overestimation of the duration of behaviours naturally causes errors in the calculations of behavioural time–energy budgets for all species that move intermittently, as demonstrated for scallops, crabs, ‘amphibious’ signal crayfish and humans. Furthermore, behaviours of any duration should be accurately detected, quantified and when appropriate, the behaviour type should be identified. The R package BEnergetix can quickly calculate accurate invertebrate and vertebrate behavioural time–energy budgets from acceleration, metabolic rate and environmental data.

KEY WORDS: Behaviour · Activity · Energy expenditure · Ecology · Accelerometer · Accuracy · R package · Crayfish · Scallop · Crab · Human

METHODS AND DISCUSSION

The daily time spent active and inactive are key factors in animal ecology and have important energetic consequences. Thus, behaviour duration should be measured accurately. The quantification of animal behavioural energetics from data recorded by animal-attached acceleration loggers is rapidly increasing in popularity (Brown et al. 2013). These accelerometers

measure the change in velocity of an animal's body over time and allow the fine-scale measurement of behaviour and body postures, unlimited by visibility, terrain, climate, observer bias or the scale of space use. Unfortunately, accelerometer data processing can cause the elongation of behaviour duration and thus an underestimation of resting duration in a behavioural time budget (e.g. Halsey & White 2010). Can the accelerometry technique be improved? Here

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we show how the accelerometry technique has and has not been used to accurately measure behaviour duration. Furthermore, we show that a consequence of the elongation of behaviour duration is the overestimation of energy expenditure.

In Robson et al. (2012), individual scallops *Pecten maximus* were instrumented with miniature data-logging devices; these recorded acceleration in 3 axes (0–6 *g*), gape angle (°) via a calibrated Hall sensor (Robson et al. 2009), depth (m) and temperature (°C), all at 16 Hz with 22-bit resolution continuously for 24 to 36 h. Fig. 1 illustrates the occasional short-burst activity typically exhibited by scallops.

A derivative of dynamic body acceleration (DBA) such as the vector sum of dynamic body acceleration

(VeDBA) can be calculated from tri-axial acceleration data recorded by a logger instrumented to a subject animal (VeDBA (*g*) = $\sqrt{(a_x^2 + a_y^2 + a_z^2)}$ where a_x , a_y and a_z are dynamic acceleration values derived from raw *x, y, z* acceleration data (Gleiss et al. 2011)). Such data represent the acceleration recorded by the logger owing to the dynamic movement of that individual (Wilson et al. 2006). DBA can be used to assess the behaviours of the animal and can also be calibrated with rate of energy expenditure. Measurements of DBA in scallops enabled Robson et al. (2012) to measure the effects of anthropogenic disturbance on the behaviour and energy expenditure of farmed individuals. To interpret scallop behaviour from the data, the entire DBA and gape angle data set was

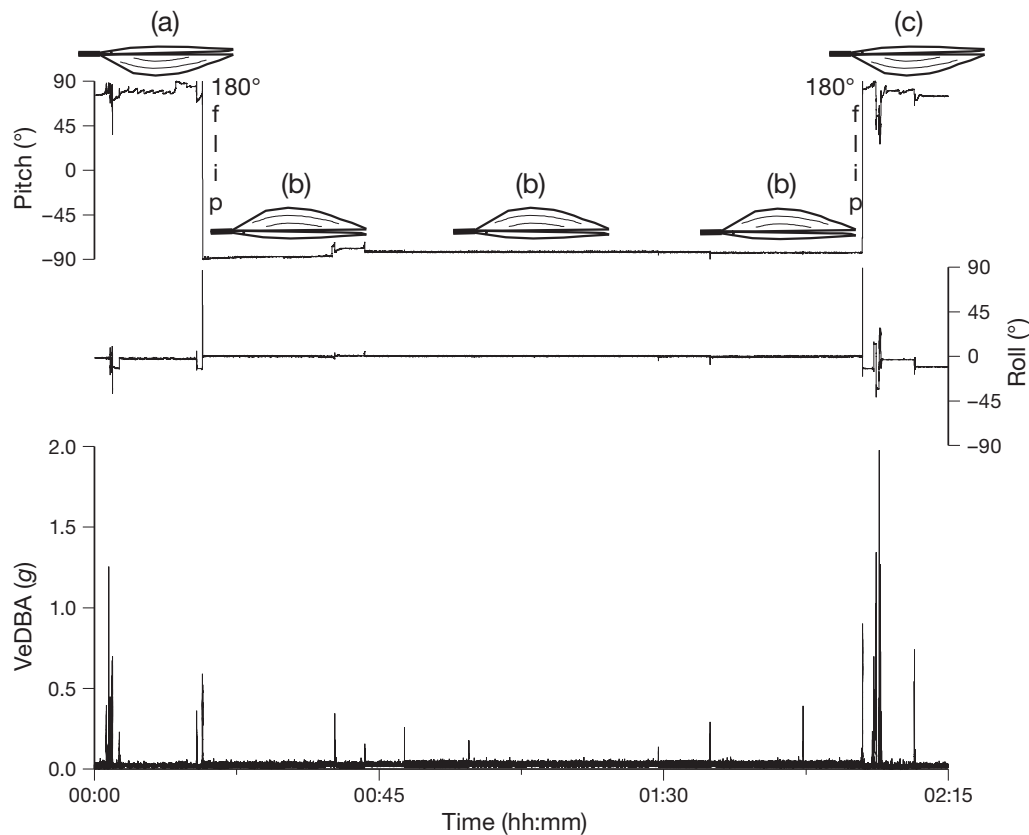


Fig. 1. Scallop *Pecten maximus* short-burst activity including two 180° flips. Top panel: body pitch derived using the equation:

$$\arctan\left(\frac{\text{static heave}}{\sqrt{\text{static surge}^2 + \text{static sway}^2}}\right).$$

Scallops (a) to (c) indicate body posture when the individual is stationary. Initially the scallop is in its typical posture in a depression in the seafloor sediment with the upper (left) valve uppermost (a) and the scallop subsequently flips 180° using rapid valve adduction followed by abduction events (2 to 3 s^{-1}) so that its upper valve is resting on the seafloor sediment (b), before flipping back to its initial posture (c). Middle panel: body roll derived using the equation:

$$\arctan\left(\frac{\text{static sway}}{\sqrt{\text{static surge}^2 + \text{static heave}^2}}\right).$$

Bottom panel: vectorial summation of scallop dynamic body acceleration (VeDBA)

plotted against time, and signatures within the trace indicating active behaviours were selected manually. DBA was selected only where a corresponding rapid change in gape angle (Robson et al. 2007) was recorded. From the manually selected DBA trace for each behaviour, the duration of the behaviour was calculated, along with the mean DBA to estimate energy cost. Furthermore, the behaviour 'type' was identified by eye both from the DBA and depth trace for each behaviour and by viewing the associated infrared video recordings. This manual analysis produces accurate behavioural time budgets, but is labour intensive for large data sets and impractical when analysing similar data recorded at high frequency from hundreds of animals. Furthermore, the Hall sensor needed to record gape angle is not a standard feature of commercial data loggers that record (tri-axial) acceleration e.g. the AXY-2 data logger (TechnoSmArt), which can record at high resolution (cf. Robson et al. 2009) for 6 wk. Thus, there is considerable value in an automated system for analysing acceleration data and without the need for the quantification of gape angle.

It is important to note that the method for calculating DBA by smoothing acceleration data using a necessarily long running mean of e.g. ≥ 1 s (Shepard et al. 2008) (the DBA method) is not appropriate for determining behaviour duration. In fact, the DBA method results in the elongation of behaviour duration (mean \pm 95% CI behaviour duration elongation for scallops ($n = 10$ animals) and humans ($n = 10$ free-ranging aquatic biologists): 508.5 ± 277.2 and $19.3 \pm 1.1\%$, respectively) and consequently an overestimation of energy expenditure (mean \pm 95% CI activity metabolic rate overestimation: 212.5 ± 48.0 and $6.12 \pm 0.34\%$, for scallops and humans, respectively; overall metabolic rate overestimation: 91.1 ± 29.9 and $4.18 \pm 0.20\%$, for scallops and humans, respectively; see Supplement 1 at www.int-res.com/articles/suppl/b021p121_supp.pdf); elongating a single crayfish, scallop and human behaviour by 22.4 (8), 2.28 (59) and 1.04 (18) s (%), respectively (Fig. 2). Fig. 2 shows that behaviour duration elongation is of greatest significance when behaviour durations are short (minimum, mean and maximum single behaviour duration for scallops and humans recorded in this study: 0.12 and 0.37, 0.40 and 8.04, 0.84 and 185.73 s, respectively). It is important to emphasise that the overestimation of the duration of behaviours is an issue for all species, that move intermittently.

Unfortunately, one root mean square (rms) DBA value (e.g. Spivey & Bishop 2013) cannot be output from each row of raw x , y , z acceleration because the

rms is calculated from N dynamic acceleration samples ($a_{x1} \dots a_{xn}$, $a_{y1} \dots a_{yn}$, $a_{z1} \dots a_{zn}$). For example if $N = 75$ (3 s when recording at 25 Hz) then rms DBA can be calculated:

$$\begin{aligned} a_1 &= (a_{x1}^2 + a_{y1}^2 + a_{z1}^2)/3 \\ a_2 &= (a_{x2}^2 + a_{y2}^2 + a_{z2}^2)/3 \\ a_3 &= (a_{x3}^2 + a_{y3}^2 + a_{z3}^2)/3 \\ \dots a_n &= (a_{xn}^2 + a_{yn}^2 + a_{zn}^2)/3 \\ \text{rms DBA} &= \sqrt{(a_1 + a_2 + a_3 + \dots + a_n) / N} \end{aligned}$$

i.e. it is a mean value calculated over multiple time points. Thus, rms DBA cannot be used to accurately measure behaviour durations because it results in the elongation of behaviour duration. Furthermore, the high-pass filtering techniques used by Spivey & Bishop (2013) to derive dynamic acceleration could overestimate behaviour duration (cf. the DBA method (Shepard et al. 2008)) before rms DBA is even calculated. Furthermore, the measure of body acceleration: total acceleration variability (Weippert et al. 2013) cannot be used to accurately measure behaviour durations because, as with rms DBA, each value is a mean calculated over multiple time points. Thus, total acceleration variability also results in the elongation of behaviour duration.

Possibly the most accurate way to measure behaviour duration (without video recordings and/or Hall sensor recordings of animal behaviour) is to calculate a 'partial' DBA (DBA_{behav}) using a running mean (moving average) of ca. 5 to 15 data points (ca. 0.2 to 0.6 s) when recording at 25 Hz. An automated system (BEnergetix—see below) is then able to accurately mark the start and end point of each behaviour within a 'DBA_{behav}' trace, validated for scallops *Pecten maximus* and *Chlamys islandica*, signal crayfish *Pacifastacus leniusculus*¹, shore crabs

¹American signal crayfish are amphibious. We have observed them moving over rough terrain, and climbing up and burrowing through brickwork. In a secure courtyard open to the sky (The Quad, Michael Smith Building, University of Manchester, UK), AXY-2 data logger-instrumented signal crayfish ($n = 11$ male, 11 female) climbed out of vertical-sided aquaculture tanks containing food and walked 83 to 465 ($\bar{X} = 223$) m d⁻¹ overland (recording duration 72 h). Furthermore, they survived on land for up to 2 wk. In addition, over 5 non-consecutive days in 2013, we opportunistically observed signal crayfish ($n = 12$ male, 8 female) leaving a lake (53.1822° N, 2.0582° W) and walking overland to other water bodies around Danebridge, UK (all crayfish subsequently captured and killed). We believe this is the first scientific corroboration of observations from fish farms and infested ponds that large numbers of 'invasive' signal crayfish can escape and disperse between patchy freshwater habitats overland (e.g. Danebridge Fisheries, UK; Radcliffe Angling Club, UK, pers. comm.)

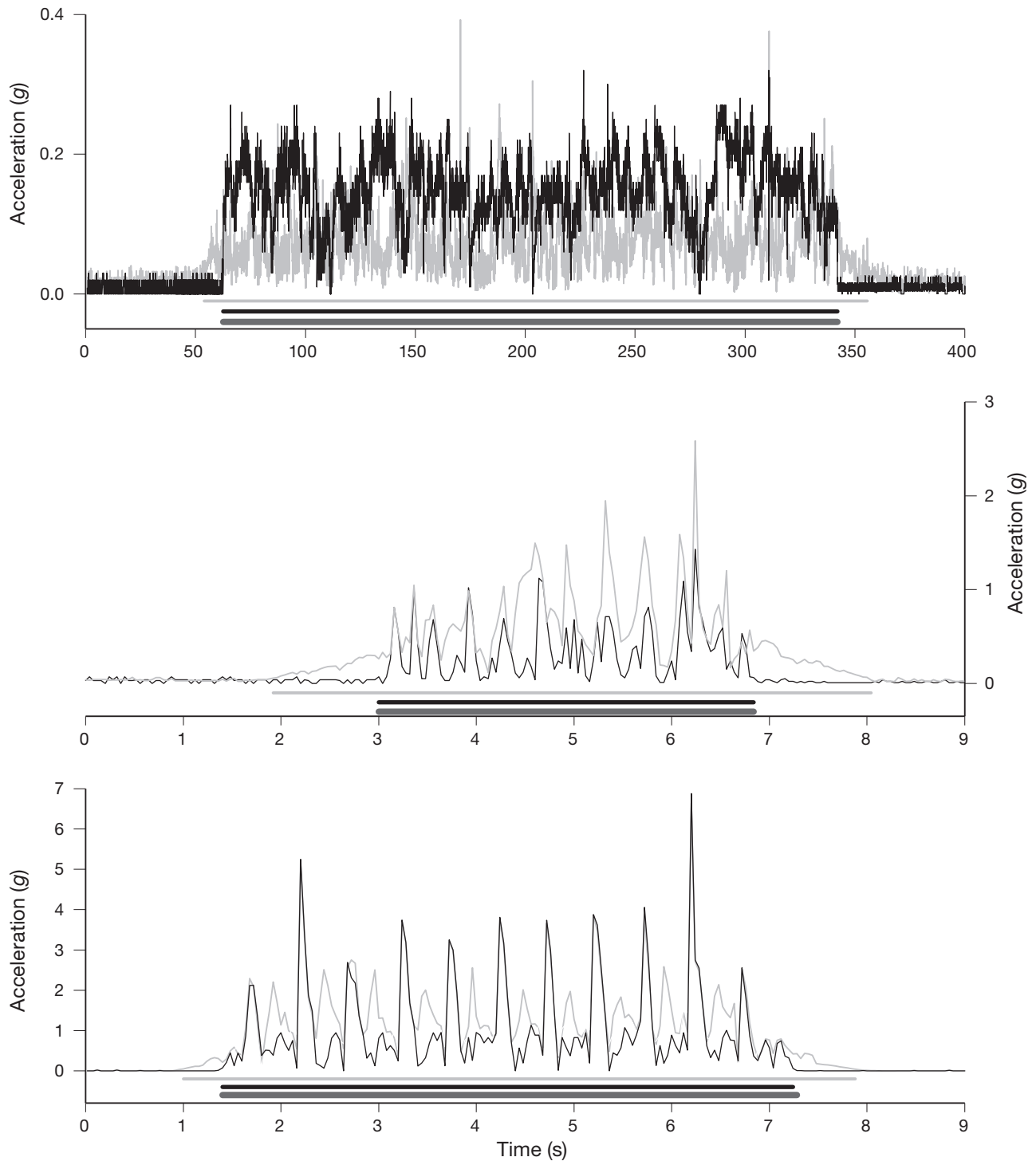


Fig. 2. Examples of the elongation of behaviour durations by vectorial summation of scallop dynamic body acceleration (VeDBA) (light grey line) derived using 'the DBA method' species/behaviour-specific running mean shown by simultaneously plotting sum absolute raw acceleration ((absolute surge + absolute sway + absolute heave) - 1) (black line). Top panel: a signal crayfish *Pacifastacus leniusculus* walking, i.e. invading overland for 279 s (running mean = 10 s). Middle panel: a scallop *Pecten maximus* spinning for 3.84 s — multiple consecutive rotations (running mean = 3 s). Lower panel: an adult female hominid *Homo sapien* star jumping (10 consecutive star jumps) for 5.84 s (running mean = 1 s). All data recorded at 25 Hz using an AXY-2 data logger (TechnoSmArt). The length of the horizontal lines below the acceleration traces in each panel indicate behaviour duration estimated from VeDBA (light grey line), actual behaviour duration (calculated manually (by eye) from the raw acceleration trace) (black line) and behaviour duration estimated using BEnergytix (dark grey line)

Carcinus maenas and humans *Homo sapiens*. Furthermore, DBAbehav and DBA are calculated simultaneously (these data are aligned). Using the behaviour markers, the 'actual' DBA trace for each behaviour is selected and the duration of the behaviour is calculated (Fig. 2), along with the mean DBA (Supplement 1).

Publications reviewed in Brown et al. (2013) report on custom-written computer programs for the analysis of animal acceleration data. However, as far as we are aware, currently these programs are still in their infancy and, we think, could be improved by more accurately calculating behaviour duration and detecting all behaviours. For example, the semantic annotation and activity recognition system (Gao et al. 2013) could be improved by processing data recorded at high sampling frequencies (e.g. 25 to 100 Hz), to discern all behaviours (Robson et al. 2009), over weeks or months. Furthermore, behaviour duration cannot be calculated accurately when acceleration is measured in blocks of 3 s (Shamoun-Baranes et al. 2012), especially when behaviour durations are short, e.g. <10 s. Automatic animal behavioural classification of acceleration data using the k-nearest neighbour algorithm (Bidder et al. 2014) can be much improved by analysing behaviours of short duration because, as this report highlights, shellfish (invertebrate) and human (vertebrate) behaviours can frequently be <1 to 10 s in duration.

We have now written a freely available R (R Development Core Team 2013) package, BEnergetix (Mansfield & Robson 2013), utilising the package Rcpp (v.0.10.6) to optimise large data set analysis (see Supplement 2 at www.int-res.com/articles/suppl/b021p121_supp.pdf). BEnergetix is easy for accelerometry beginners to use to quickly calculate behavioural time–energy budgets from acceleration, metabolic rate and environmental data. The beta version of BEnergetix, its algorithms and a user manual are freely available from Mansfield & Robson (2013). BEnergetix analyses large data sets recorded at high frequency (e.g. 100 Hz) limited only by available computer memory (RAM), although future releases will seek to remove this limitation (cf. Sakamoto et al. 2009, Nathan et al. 2012, Shamoun-Baranes et al. 2012, Gao et al. 2013). In conclusion, the overestimation of the duration of behaviours naturally causes errors in the calculations of behavioural time–energy budgets for all species that move intermittently. Furthermore, behaviours of any duration should be accurately detected, quantified and, when appropriate, the behaviour type should be identified.

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