Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector?

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Abstract

Dynamic body acceleration (DBA) has been used as a proxy for energy expenditure in logger-equipped animals, with researchers summing the acceleration (overall dynamic body acceleration - ODBA) from the three orthogonal axes of devices. The vector of the dynamic body acceleration (VeDBA) may be a better proxy so this study compared ODBA and VeDBA as proxies for rate of oxygen consumption using humans and 6 other species. Twenty-one humans on a treadmill ran at different speeds while equipped with two loggers, one in a straight orientation and the other skewed, while rate of oxygen consumption ($V\dot{O}_2$) was recorded. Similar data were obtained from animals but using only one (straight) logger. In humans, both ODBA and VeDBA were good proxies for $V\dot{O}_2$ with all $r^2$ values exceeding 0.88, although ODBA accounted for slightly but significantly more of the variation in $V\dot{O}_2$ than did VeDBA (P<0.03). There were no significant differences between ODBA and VeDBA in terms of the change in $V\dot{O}_2$ estimated by the acceleration data in a simulated situation of the logger being mounted straight but then becoming skewed ($P = 0.744$). In the animal study, ODBA and VeDBA were again good proxies for $V\dot{O}_2$ with all $r^2$ values exceeding 0.70 although, again, ODBA accounted for slightly, but significantly, more of the variation in $V\dot{O}_2$ than did VeDBA (P<0.03). The simultaneous contraction of muscles, inserted variably for limb stability, may produce muscle oxygen use that at least partially equates with summing components to derive DBA. Thus, a vectorial summation to derive DBA cannot be assumed to be the more 'correct' calculation. However, although within the limitations of our simple study, ODBA appears a marginally better proxy for $V\dot{O}_2$. In the unusual situation where researchers are unable to guarantee at least reasonably consistent device orientation, they should use VeDBA as a proxy for $V\dot{O}_2$.

Introduction

The broad interest in animal optimal foraging [1] underpins the central concept that creatures should behave in such a way as to maximize their inclusive fitness by maximizing their net rate of energy intake [see 2,3]. This includes optimized harvesting solutions [e.g. 4,5,6] but also minimizing locomotion costs in animals that have to move to acquire food [7]. Thus, information on the rate at which organisms expend energy during movement is fundamental to informing models of optimal foraging and indeed, ultimately, the efficiency of movement affects the survival of wild animals [8]. Understanding optimality in foraging is only one example that demonstrates the importance of being able to determine energy expenditure but it, like many other biological processes, is best informed by energy expenditure at a fine-scale temporal resolution, something that is notably rare in published studies with some exceptions [9,10,11,12]. This situation stems from a paucity of appropriate methods for determining the power use of wild animals.

The most common methods of measuring animal energy expenditure have used doubly labelled water (DLW) [13,14,15,16,17], direct and indirect calorimetry [e.g. 18], or some proxy for energy expenditure such as heart beat rate (fH) [19,20,21,22,23]. All the above systems have disadvantages [reviewed by 20,24] which disill out into giving poor temporal resolution (doubly labelled water), being confined to a laboratory situation (calorimetry) or generally involving invasive methods of instrumentation (heart rate). See Halsey [25] and references therein for further details.

Beyond these approaches, however, some researchers have examined the use of mechanical motion sensors [26,27] in studies of animal power use. In fact, as early as 1963, researchers proposed that the extent of body movement should act as a proxy for energy expenditure [28] because in order to elicit movement,
animals need to expend energy, with more pronounced and vigorous movements presumed to arise as a result of more energy expended [e.g. 29,30,31]. Thus, specifically, energy expenditure should correlate with the extent of movement in some manner [32,33]. In 2006, an acceleration-based proxy for energy expenditure focusing on dynamic body acceleration (DBA) was proposed, using tri-axial acceleration data derived from a logger recording at high rates (>10 Hz) and placed close to the participant’s centre of gravity [34]. The specific proxy for metabolic rate was overall dynamic body acceleration (ODBA), determined by adding the dynamic acceleration from three orthogonally-placed accelerometers orientated so as to represent the main axes of the animal’s body; in the surge, heave and sway dimensions [34]. Although this original work was conducted on birds, subsequent studies confirmed linear, strong correlations between the rate of oxygen consumption ($V_O_2$) and ODBA in fish [35], amphibians [36], birds [34,37,38] and mammals [12,39], including man [39].

Despite the promise of the newly proposed ODBA method, however, Gleiss, Wilson et. al. [24] point to an uncertainty in its formulation. Actually, acceleration is a vectorial quantity so it might seem incorrect that ODBA should treat each axis as independent because the implication is that the ODBA metric represents work done by three distinct straight-line paths and thus overestimates the work done for any specific movement. Furthermore, ODBA values are expected to differ according to the alignment of the axes of the logger with respect to the equipped participant, something that should not affect a vectorial solution [24]. The suggestion, therefore, is that properly calculated vectorial dynamic body acceleration ($VDBA$) may, in fact, prove a better, and a more appropriate proxy for metabolic rate than does ODBA. Indeed, a recent study by McGregor, Busa et al. [40] uses $VDBA$ (although not referred to as such) rather than ODBA as a proxy of $V_O_2$. On the other hand, from a mathematical perspective both ODBA and $VDBA$ are norms and so are equally valid ways to measure the length of a vector. To ascertain which derivative is a better proxy of $V_O_2$ is difficult because there is no expected mathematical relationship that can be examined to calculate the impact of using different norms. Furthermore, the empirical relationship will depend on the species, the data logger location on the animal, and the behaviour and locomotion gait(s) of the animal. Thus a direct test of the predictive power of ODBA and $VDBA$ is required, yet Gleiss, Wilson et al. [24] note that no studies have explicitly sought to determine whether ODBA or $VDBA$ is a better predictor of metabolic rate and whether the outcome of such a test might be influenced by logger orientation on the animal.

The present study attempts to determine whether ODBA or $VDBA$ is a better proxy for rate of oxygen consumption. Humans are used as a model species [cf. 39] and primary data collected while people move at different speeds on a treadmill are analysed in detail. This is supplemented by reanalysis of published data [12] for six other animal species. The implications of the findings are discussed in terms of the most appropriate way to derive dynamic body acceleration in the future.

Materials and Methods

The human study

Twenty-one healthy adults (mean age ± SD: 20.44±3.28 years) were involved in the study. Before the start of the experiment, the height (1.75±0.07 m) and weight (70.66±9.78 kg) of the participants were measured according to the International Standards for Anthropometric Assessment (2001). The experimental protocol was approved by the Swansea University Ethics Committee. All participants were asked to give informed consent before the trials began.

Broadly, the investigations compared the rate of oxygen consumption during locomotion by humans on a treadmill while back-mounted loggers recorded tri-axial acceleration.

Specifically, all participants performed a VO$_2$ max test [40] on a treadmill (Woodway Ergo ELG 53; Woodway GmbH, Germany) that started at 3 km/h and increased in speed every 5 min by 1 km/h until participant volitional exhaustion. During this process the participants breathed into a mask, and expired air was analyzed for oxygen and carbon dioxide content using an Oxycon Pro (Jaeger Oxycon Mannual Version 4.5, VIASYS Healthcare GmbH, Hoechberg, Germany) on a breath-by-breath basis. Acceleration was measured using two tri-axial accelerometers (X6-1A USB; Gulf Coast Data Concepts, LLC, Waveland, USA; 16 bit resolution, recording range ±6 g), each set to record at 96 Hz on each of the three orthogonal axes. The loggers were placed within holding moulds cut into a single poly styrene saddle to ensure correct orientation; one unit was mounted in accordance with the main body axes of surge, heave and sway while the other was set to be 30° displaced from this for all axes. This skew-mounted accelerometer was rotated by 30° about the roll, pitch and yaw axes respectively, where the roll axis was taken as the long axis of the accelerometer. The saddle was optimised by trial and error during pilot studies to move properly with the participant’s body. It was placed in the centre of the participant’s back between the shoulder blades and held in place using a specially made Silastic® (Silastic® P1 Base and Curing Agent, Thomson Bros Newcastle Ltd) harness which kept the system in a stable position even during the most vigorous of movement.

The animal study

Data previously gathered comparing $V_O_2$ with acceleration data for animals during activity on a treadmill at Buenos Aires Zoo [12] were reanalyzed to supplement the work on humans. Species used were; coypu (Myocastor coypus) (4 individuals), larger hairy armadillo (Chlamyphorus truncatus) (1 individual), Muscovy duck (Cairina moschata) (1 individual), greylag goose (Anser anser) (2 individuals), Magellanic penguin (Spheniscus magellanicus) (2 individuals) and rockhopper penguin (Eudyptes chrysolophus) (1 individual). Briefly, animals were equipped with acceleration data loggers, attached variously, before being exposed to a treadmill with the tread moving at a range of speeds between 0 and 2.52 km/h, the upper limit dependent on their capacities. The animals were given rests between the higher speeds where the predominant behavior was locomotion however at the lower speeds the animal typically exhibited a range of behaviors including searching, scratching and lying. An open circuitry respirometry system was used to measure $V_O_2$. Full details of the protocol are given in Halsey et al. [12].

Data analysis

The raw accelerometer data were converted to DBA by first smoothing each channel to derive the static acceleration using a running mean over 2 s [7] and then subtracting this static acceleration from the raw data [24]. The resulting values for dynamic acceleration were all then converted to positive values. These values for DBA were then either summed to provide ODBA [34]:

$$ODB A = |A_x| + |A_y| + |A_z|$$

where $A_x$, $A_y$ and $A_z$ are the derived dynamic accelerations at any
point in time corresponding to the three orthogonal axes of the accelerometer, or their vectorial sum (VeDBA) using:

\[ VeDBA = \sqrt{A_x^2 + A_y^2 + A_z^2} \]  

Means for ODBA and VeDBA were derived for all data corresponding to particular running speeds (for each individual used in the experiments) and plotted against speed and VO₂. Because measurements of VO₂ are most indicative of rate of energy expenditure when metabolism is mainly aerobic, VO₂ and VO₂ were also plotted against one another and the gas exchange threshold determined for each human participant using the v-slope method [41]: The plot of VO₂ and VO₂ typically shows two slopes corresponding to the way VO₂ changes with respect to VO₂ and the point at which these slopes intersect is considered to be the gas exchange threshold, which closely corresponds to the ventilatory threshold [41,cf. 42], the point which approximately indicates when the participant changes from aerobic to anaerobic respiration as a main source of energy production. All data where participants were running at speeds which suggested that there was considerable anaerobic metabolism were excluded from the analysis.

Simple linear regressions were used to test the strength of relationships between ODBA and VeDBA for both humans and animals. Mixed linear models tested the relationships between data recorded from the straight mounting and data recorded from the skewed mounting in the human trials. The coefficient of variation for ODBA and VeDBA was calculated for each human participant for the two logger data sets combined. Mixed linear models were used to generate equations for VO₂ against the two acceleration metrics for all participants together, including participant as a random factor, separately for the straight- and skew-mounted logger data. To compare the error on estimates of VO₂ using ODBA or VeDBA caused by an acceleration logger becoming skewed, the difference between measured VO₂ and VO₂ estimated by a skew-mounted logger using calibrations for a straight-mounted logger at speed 5 (an average walking speed) was calculated for both these derived metrics. Paired tests were used to test for differences between ODBA and VeDBA. Mean values are provided ±1 S.E. (standard error).

**Results**

**The human study**

The accelerometers recorded a very precise profile of tri-axial acceleration from each participant during walking and running (Fig 1) with clear peaks in heave and surge in particular, denoting each stride, although peaks in sway were also apparent.

Gas analytical data and data from the straight-mounted logger were obtained for all participants, while data from the skew-mounted logger were obtained for 13 of the participants (on three occasions the logger failed). Q-Q plots indicated that the distribution for all the VO₂ data together was reasonably normal. ODBA and VeDBA appeared non-normally distributed as did the values representing the percentage change in estimated VO₂ due to the logger becoming skewed. However, for the majority of analyses, ODBA and VeDBA represented the independent variable. The r² values for VO₂ against ODBA and VeDBA for both straight and skewed logger orientations were reasonably normal.

For all participants and both logger mountings, ODBA and VeDBA from trials were highly correlated with each other (Figs. 2 and 3), with r² values on means derived from all participants typically being ca. 0.999. Mixed linear models (straight ODBA—skewed ODBA+participant(random), or, straight VeDBA—skewed VeDBA+participant(random)) indicated that during the trials, ODBA values from the straight-mounted devices were highly correlated with the ODBA values from the skew-mounted devices (r² = 0.99), as were VeDBA values from the straight- and skew-mounted devices (r² = 0.99) (Fig. 4). Both ODBA and VeDBA were highly correlated with VO₂ (Fig. 5). Mixed linear models (VO₂—ODBA+participant(random), or, VO₂—VeDBA+participant(random)) returned significant relationships for both the straight and the skewed mountings (Table 1).

ODBAs accounted for significantly more of the variation in VO₂ than did VeDBA for the straight-mounted loggers (mean r², ODBA: 0.95±0.01; VeDBA: 0.94±0.01; t₂₀ = 2.29, P = 0.03) and for the skew-mounted logger (t₁₇ = 2.44, p = 0.03) (mean r², ODBA: 0.94±0.01; VeDBA: 0.91±0.01). The difference in r² values for single linear regressions of VO₂ against ODBA versus VO₂ against VeDBA for each participant, for both the straight-mounted logger and the skewed logger, are very small. 95% confidence intervals derived from paired t tests indicate that the true difference in r² for the straight-mounted logger is in the range of 0.0004 to 0.0078, while for the skew-mounted logger is in the range of 0.0003 to 0.0040. These ranges represent less than 0.1% of mean r² values.

To test for differences between ODBA and VeDBA in the effect on estimates of VO₂ in the case of an initially straight-mounted logger subsequently becoming skewed VO₂ measured during speed 5 on the treadmill was compared to VO₂ estimated from acceleration measurements recorded by the skew-mounted logger using the straight-mounted logger calibrations. For both ODBA and VeDBA the percentage difference between VO₂ measured and VO₂ estimated was small (median, ODBA: 0.93; VeDBA: 0.81), and...
the size of this difference was similar for the two metrics (Wilcoxon signed ranks test: $Z = 2.037$, $N = 18$, $P = 0.744$).

Table 1. Overall relationships between $\text{VVO}_2$ and $\text{ODBA}$ or $\text{VeDBA}$ recorded for humans locomoting on a treadmill using an acceleration logger in a straight orientation or a skewed orientation.

The animal study
In a manner similar to the human study, the coefficients of determination for the relationships between $\text{ODBA}$ or $\text{VeDBA}$ and $\text{VVO}_2$ were all high, ranging between $r^2 = 0.70$ for the $\text{VeDBA}$ versus $\text{VVO}_2$ relationship for coypu 4 and $r^2 = 0.99$ for the $\text{VeDBA}$ versus $\text{VVO}_2$ relationship for the rockhopper penguin (Table 2). The $\text{ODBA}$ values had significantly higher coefficients of determination than the $\text{VeDBA}$ values ($t = 2.54$, $P = 0.03$).

Table 2. $r^2$-values for relationships between $\text{ODBA}$ or $\text{VeDBA}$ and $\text{VVO}_2$ recorded using an acceleration data logger on a range of animals during activity at Buenos Aires Zoo.

Discussion
In the purely physical sense, $\text{ODBA}$ and $\text{VeDBA}$ are derived using the same terms and, although the relative importance of the
whether they differ minimally (Table 2). This makes the discussion of
between that an important finding of this study is the close correlation
[38,43]. With these provisos in mind, generally, it is to be expected
explicitly sought to incorporate behaviours other than straight-line
correlations between always being less than 1. In addition, simple comparisons of the
straight loggers with, unsurprisingly, the slope of the relationship
of less than 0.998 for mean values derived from either skew or
values will generally also accompany larger
VeDBA terms differs, the precise formulation of them means that larger
VeDBA values will generally also accompany larger ODBA values, although VeDBA values will almost invariably be lower and never
higher than ODBA. How much higher ODBA is than VeDBA will depend,
inter alia, on the type of motion recorded which, in turn
depends on animal type, gait and tag location. Our study was
limited in scope, incorporating data from only 7 species, all of
which were travelling in a straight line on a treadmill (although
some species exhibited a range of behaviors at slower speeds), so it
is unwise to over-interpret. Nonetheless, the treadmill approach
has been used as a general method to simulate increased activity of
types in animals show

\[ \text{Table 1. Overall relationships between } \dot{V}O_2 \text{ and ODBA or VeDBA recorded for humans locomoting on a treadmill using an acceleration logger in a straight orientation or a skewed orientation.} \]

|        | Straight       | Skewed        |
|--------|----------------|---------------|
| ODBA   | VO2 = 1132.0DBA+615 \(r^2 = 0.915\) | VO2 = 1466.0DBA+776 \(r^2 = 0.94\) |
| VeDBA  | VO2 = 1664.0VeDBA+636 \(r^2 = 0.914\) | VO2 = 1659.0VeDBA+629 \(r^2 = 0.91\) |

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differences in the utility of ODBA with respect to VeDBA [24], the
present study was conducted to carry out tests into the matter.

Vectorial versus summed tri-axial acceleration as a proxy for \(\dot{V}O_2\)

From a theoretical standpoint it may seem perplexing that
VeDBA does not outperform ODBA as a proxy for \(\dot{V}O_2\) and a
specific explanation is warranted. If the simple scenario of one
limb articulating on another is considered (Fig. 6) where muscles
emanating from the upper limb are inserted at various angles \(\theta\)
on the lower limb [e.g. 44], each exerting a force \(F\), then the
overall force along the longitudinal y-axis \(F_{y\text{tot}}\) is given by the
vectorial solution;

\[ F_{y\text{tot}} = \sum_{i=1}^{n} F_i \cos \theta_i \]  

where the subscripts refer to each of the specific muscles with their
defined forces and angles of insertion relative to the y-axis of the
lower limb. In a similar manner, the total force along axis x is;

\[ F_{x\text{tot}} = \sum_{i=1}^{n} F_i \sin \theta_i \]  

The torque \(\tau\) along the y-axis produced by the contraction of
these muscles depends on the overall force generated along that
axis by each muscle (Eq 3) and the moment arm \(d\), defined as the
perpendicular distance between the line of action of the muscle
force and the pivot point of the articulation so that;

\[ \tau = \sum_{i=1}^{n} F_i d_i \cos \theta_i \]  

The torque is related to the angular acceleration \(\alpha\) via;

\[ \alpha = \frac{\tau}{I} \]  

where \(I\) is the moment of inertia. The linear acceleration \(a\)
perceived by an accelerometer placed on the moving lower limb is
dependent on the distance between pivot and transducer \(r\) by;

\[ a = \frac{\tau r}{I} \]  

Thus, the (linear) acceleration perceived by an accelerometer
mounted in the y-axis and measuring in the plane of movement
can be determined by substituting Eq (5) into equation (7) and is
approximated by;

\[ a = \frac{I}{\sum_{i=1}^{n} F_i d_i \cos \theta_i} \]  

which is clearly a vectorial solution. However, the work done \(W\)
during muscular contraction to produce the forces necessary for
the movement is given by;

\[ W = F \cdot \Delta D \]  

for each muscle involved, where \(\Delta D\) is the distance contracted.
The total amount of energy used during contraction by all the

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|----------------|----------------|
| Species        | ODBA           | VeDBA          |
| Chaetophractus villosum | 0.9775         | 0.942          |
| Myocastor coypus 1   | 0.9594         | 0.94           |
| Myocastor coypus 2   | 0.7449         | 0.7019         |
| Myocastor coypus 3   | 0.9473         | 0.9486         |
| Myocastor coypus 4   | 0.8617         | 0.8568         |
| Cairina moschata     | 0.9853         | 0.9841         |
| Anser anser 1        | 0.9022         | 0.8904         |
| Anser anser 2        | 0.9427         | 0.9242         |
| Spheniscus magellanicus 1 | 0.975          | 0.9662         |
| Spheniscus magellanicus 2 | 0.8979         | 0.811          |
| Eudyptes chrysocone  | 0.9914         | 0.9957         |
muscles involved in moving the limb ($W_{\text{tot}}$) is:

$$W_{\text{tot}} = \sum_{i=1}^{n} F_i \Delta D_i \quad (10)$$

a necessarily non-vectorial derivation, where the energy used equates directly with the oxygen consumed [45]. Thus, seen from a pure physics perspective, VeDBA is the proper way to derive the total magnitude of the acceleration vector at any one moment in time. However, the issue of interest to biologists studying energetics is not the total acceleration but how the DBA signal relates to rate of energy expenditure, and specifically the rate of energy expenditure used by the muscles involved. The rate of energy expenditure is not just dependent on the movement arc, which is described by VeDBA [see 24 for treatment of this], but also dependent, among other things, on the force exerted by the contracting muscles at the points of their insertion. A single muscle can contract to produce a movement arc of one limb by exerting an appropriate force (Fig. 6) while exactly the same movement arc can result from the contraction of two or more differently inserted muscles (Fig. 6), each of which exerts a force that leads to a vectorial solution that accords with that exhibited by the single muscle. In both cases the overall result for movement and physical work done is the same but in the latter case the oxygen consumed by the multiple muscles will exceed that of the single muscle because forces are developed that are not equally manifest in the movement. Fundamental to the amount of oxygen used by a body is the amount of muscular tissue that is active [46] and the precise orientation of various muscle groups involved in limb movement is critical in this regard. Human walking and running is brought about by a complex interplay of interacting, and variously inserted, muscles [44] which, nonetheless, produces a relatively simple movement arc which equates to the vectorial component of the variously contracting muscles even though the muscular work produced may more appropriately be represented by a sum value of muscular contraction. The 'inefficiencies' that result from partially opposing contracting muscles are, in fact, necessary for increasing limb stability [cf. 8]. For example, animals moving over rough terrain could not afford to have limb movement that is overly sensitive to lateral forces.

**Skew versus straight-mounted logger orientation**

A specific concern, and one that perhaps might lead to the greatest discrepancy between ODBA and VeDBA, is what happens when device orientation is not standardized. Importantly, in our study on humans, the difference in recorded $V_{O_2}$ at a speed of 5 km/h compared to $V_{O_2}$ estimated for the same speed from the data recorded by the skew-mounted logger using the calibrations obtained from the straight-mounted logger was small. Further, it did not differ between ODBA and VeDBA. Thus, apparently, even if a logger is deployed in the straight position but then subsequently slips out of true, perhaps, for example, due to the intensity of the exercise, both ODBA and VeDBA would appear similarly powerful proxies for $V_{O_2}$. In fact, contrary to what might be expected from a purely physical treatise, VeDBA did not outperform ODBA based on any of statistical analyses conducted.

The actual acceleration values recorded by a straight- with respect to skew-mounted tri-axial accelerometer can be derived for any scenario by considering the relative rotations for each of the axes. Here, the matrix representation for the acceleration vector transformation is

$$M = \begin{pmatrix} \cos \alpha \cos \beta & \cos \alpha \sin \beta \sin \gamma + \sin \alpha \cos \gamma & -\cos \alpha \sin \beta \cos \gamma + \sin \alpha \sin \gamma \\ -\sin \alpha \cos \beta & -\sin \alpha \sin \beta \sin \gamma + \cos \alpha \cos \gamma & \sin \alpha \sin \beta \cos \gamma + \cos \alpha \sin \gamma \\ \sin \beta & -\cos \beta \sin \gamma & \cos \beta \cos \gamma \end{pmatrix} \quad (11)$$

where $\alpha, \beta$ and $\gamma$ are the angles of roll, pitch and yaw angles of the skew-mounted accelerometer relative to the straight-mounted one, where the rotations are carried out in that order.

Thus, if the acceleration vector measured by the device in the straight-mounted position is

$$A_1 = (A_{1x}, A_{1y}, A_{1z}) \quad (12)$$

then in the skew-mounted position, that same acceleration is measured as a vector:

$$A_2 = (A_{2x}, A_{2y}, A_{2z}) \quad (13)$$

where

$$A_2 = MA_1 \quad (14)$$

Derived values for these vector components can be used to produce VeDBA, (using Eq 2) which does not change with orientation and, more particularly, to produce ODBA (using Eq 1) which does change with orientation (Fig. 7). This approach shows that under given conditions of triaxial acceleration (the case shown...
in Fig. 7 shows equal amounts of dynamic acceleration in the heave surge and sway axes), deviations of up to $10^\circ$ in any one axis produce only up to a 1% change in ODBA (although a 10% change in two or three axes simultaneously produces about a 1% and 0.03% change in ODBA, respectively). In fact, to produce a 5% change in ODBA requires skew placement of >$20^\circ$ in one or more axes, something which would be immediately obvious during many device attachment protocols. Thus, although many situations where loggers containing tri-axial accelerometers are attached to animals for derivation of energy expenditure will not have to worry overly about orientation [e.g. 47], there are a number of obvious situations, such as having round, unmarked devices in which the orientation of the transducers is unclear and placing devices via suction cups onto whales [48,49] that should only use $V_d$DBA. Importantly though, the latter situation is also likely to incur substantial additional errors in any derivation of DBA and its relation to $V_O2$ resulting from the non-standardized positioning of the device on the body relative to the animal’s centre of gravity, which would markedly affect both ODBA and $V_d$DBA signals [24]. This effect is apparent even in our results on humans where, despite placing the straight and skew tag as closely together as we could, the correlation coefficient between $V_O2$ and $V_d$DBA for straight and skewed tag orientations was (marginally) different. Allusion to this phenomenon, in an albeit simplistic form, can be accessed via equation (7) which shows the extent to which distance from the pivot point (or distance from the moving body part such as a fish’s tail [24]) affects DBA.

Overall, our results showed that ODBA was insensitive to the accelerometer when its axes were skewed off the major axes of the body (by $30^\circ$ in roll, pitch and yaw), which we attribute to the general variance between $V_O2$ and DBA and the fact that the degree of skew tested was insufficient to elicit a marked difference in the way ODBA reacts to changes in orientation. Thus, against predictions based on physical theory, our study indicates that ODBA is, in fact, not worse than $V_d$DBA at predicting $V_O2$ if anything it is better (though the difference is minimal) as long as devices can be attached close to the major axes of the body. This indicates that whether researchers use ODBA or $V_d$DBA may not be the most critical issue in treatment of DBA signals and $V_O2$ because variation in device positioning is likely to introduce much more variability [39]. Future work will have to address this aspect more carefully.

For the moment, researchers should certainly be working towards positioning their devices in the same anatomical location as far as possible and, with the exception of a few species such as cetaceans [47] and animals that have tags implanted [50], this will tend to lead to device orientation being correct anyway. There are other particularly germane reasons for researchers to orientate devices on their study species in a comparable manner. In particular, it underpins powerful behaviour identification protocols based on posture and dynamic acceleration [51], a process which, itself, requires device orientation to be controlled rigorously. Subsequently, both the known behaviour and the ODBA-derived estimate of metabolic rate can be used to determine activity-specific metabolic rate. $V_d$DBA would, however, clearly be a better proxy of $V_O2$ than ODBA where device orientation cannot be maintained within a $30^\circ$ arc in any of the angular dimensions and so should be used when loggers cannot be implanted [52] reasonably precisely, or attached reasonably precisely [50], or are ingested [e.g. 53]. Importantly though, determination of behaviour using inconsistently placed accelerometers is more problematic.

Conclusions

The assumption that DBA derived by a vectorial rather than an absolute summation is more appropriate as a proxy for $V_O2$ is not founded for devices mounted in a standardized manner and issues of force generation by muscles likely account for this rather than just the physics associated with measures of acceleration. ODBA and $V_d$DBA are very closely correlated with each other and both can be excellent proxies for movement-based metabolic rate. Proponents of DBA as a proxy of metabolic rate must choose which derivation to use based on (a) the value they place on the derivation representing the biology of muscle metabolism (b) whether they are concerned that logger orientation could vary markedly (c) whether they wish to compare their DBA values with values in the literature. Critically, neither ODBA nor $V_d$DBA deals with the problem of variation in device positioning.

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Author Contributions

Conceived and designed the experiments: RW. Performed the experiments: LQ RW AC AW IG. Analyzed the data: LH. Contributed reagents/materials/analysis tools: LQ RW AC AW IG. Wrote the paper: LQ AW RW IG. Gave conceptual advice: AG.

Figure 7. Predicted difference between straight- and skew-mounted ODBA derived from recordings on a tri-axial accelerometer subjected to equal acceleration in the heave, surge and sway axes as a function of pitch, roll and yaw differences between straight and skew. Contour lines show 2.5% intervals. doi:10.1371/journal.pone.0031187.g007
