Accelerometers can measure total and activity-specific energy expenditures in free-ranging marine mammals only if linked to time-activity budgets

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Summary

1. Energy expenditure is an important component of foraging ecology, but is extremely difficult to estimate in free-ranging animals and depends on how animals partition their time between different activities during foraging. Acceleration data have emerged as a new way to determine energy expenditure at a fine scale but this needs to be tested and validated in wild animals.

2. This study investigated whether vectorial dynamic body acceleration (VeDBA) could accurately predict the energy expended by marine predators during a full foraging trip. We also aimed to determine whether the accuracy of predictions of energy expenditure derived from acceleration increased when partitioned by different types of at-sea activities (i.e. diving, transiting, resting and surface activities).

3. To do so, we equipped 20 lactating northern (*Callorhinus ursinus*) and 20 lactating Antarctic fur seals (*Arctocephalus gazella*) with GPS, time-depth recorders and tri-axial accelerometers and obtained estimates of field metabolic rates using the doubly labelled water (DLW) method. VeDBA was derived from tri-axial acceleration, and at-sea activities (diving, transiting, resting and surface activities) were determined using dive depth, tri-axial acceleration and travelling speed.

4. We found that VeDBA did not accurately predict the total energy expended by fur seals during their full foraging trips ($R^2 = 0.36$). However, the accuracy of VeDBA as a predictor of total energy expenditure increased significantly when foraging trips were partitioned by activity and when activity-specific VeDBA was paired with time-activity budgets ($R^2 = 0.70$). Activity-specific VeDBA also accurately predicted the energy expenditures of each activity independent of each other ($R^2 > 0.85$).

5. Our study confirms that acceleration is a promising way to estimate energy expenditures of free-ranging marine mammals at a fine scale never attained before. However, it shows that it needs to be based on the time-activity budgets that make up foraging trips rather than being derived as a single measure of VeDBA applied to entire foraging trips. Our activity-based method provides a cost-effective means to accurately calculate energy expenditures of fur seals using acceleration and time-activity budgets, that can be transfered to studies on other species.

Key-words: acceleration, Antarctic fur seal, energy expenditure, foraging, metabolic rate, northern fur seal, time-activity budget, VeDBA

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Introduction

Predators constantly make decisions on where to hunt, what to hunt and for how long to hunt that collectively affects the efficiency with which they obtain energy and minimize foraging costs (MacArthur & Pianka 1966; Perry & Pianka 1997; Sayers & Menzel 2010). It is this foraging efficiency, or the cost-benefit ratio of foraging, that drives many aspects of the physiology, biology and ecology of wild animals, which in turn affects their health, reproduction and survival (Lescroël *et al.* 2010). It is, thus, important to accurately estimate foraging costs to understand and predict survival and reproductive success at the individual and population levels (Boyd 2002), or to calculate food requirements and understand predator–prey interactions (Lavigne *et al.* 1982; Winship, Trites & Rosen 2002; Halsey & White 2010).

Heart rate monitors, accelerometers and doubly labelled water (DLW) have all been used to measure energy expenditure in vertebrates (Lifson & McClintock 1966; Butler *et al.* 1992; Butler 1993; Speakman 1997; Froget *et al.* 2004; Wilson *et al.* 2006; Young *et al.* 2011). However, heart rates and DLW measurements can be invasive, very costly, have their own biological limitations and are often impractical for large wild animals (Nagy 1980; Thorarensen, Gallaugher & Farrell 1996; Ward *et al.* 2002; Butler *et al.* 2004; Dalton, Rosen & Trites 2014). In addition, these techniques are not readily applicable to large sample sizes or across the different temporal scales that are required in many ecological studies. More recently, accelerometry techniques have emerged in the field of ecological energetics and have the potential to provide valuable fine-scale information over days, weeks or months. This is why simple measures of body movement from accelerometry are increasingly being sought to estimate energy expended by animals

The overall dynamic body acceleration (ODBA) and vectorial dynamic body acceleration (VeDBA) are two very similar tri-axial body acceleration metrics that can be linked to energy expenditure (Wilson *et al.* 2006; Halsey *et al.* 2009a,b; Qasem *et al.* 2012). ODBA and VeDBA have been tested and calibrated on various taxa, whether marine or terrestrial, endotherms or ectotherms during different types of activities (walking, flying, swimming etc., Fahlman *et al.* 2008; Halsey *et al.* 2008; Gleiss, Gruber & Wilson 2009; Halsey & White 2010; Gomez-Laich *et al.* 2011; Halsey *et al.* 2011). They appear to have acceptable accuracy for determining energy expenditure, but relationships between acceleration and energy expenditure vary by species and by type of activity and need to be calibrated for each case (Halsey *et al.* 2008; Elliott *et al.* 2013; Wright *et al.* 2014). They also need to be tested with free-ranging animals undertaking their full suite of natural activities under different environmental conditions.

Establishing the relationship between ODBA/VeDBA and energy expenditure is particularly difficult for air-breathing divers due to a possible uncoupling of acceleration and gas exchange. This uncoupling can arise from variations in buoyancy, use of gliding or other physiological functions (i.e. thermoregulation, digestion etc., Gleiss, Wilson & Shepard 2011; Halsey, Shepard & Wilson 2011). Differences in resistance between air and water may also create different relationships between acceleration and energy expenditure, and there may be effects of wind and waves at surface on acceleration that are not reflected in energy expenditure (Gomez-Laich *et al.* 2011; Halsey, Shepard & Wilson 2011).

Most validation and calibration studies of ODBA/VeDBA have been conducted in controlled environments over short periods, which might buffer the above limitations. For example, ODBA correlates with energy expenditure of semi-captive Steller sea lions (*Eumetopias jubatus*) trained to dive at sea (although with an R^2 of 0·47, Fahlman *et al.* 2008), but does not correlate with the daily metabolic rate of captive northern fur seals over a 5-day period (Dalton, Rosen & Trites 2014). This suggests that the predictive power of ODBA may decrease as time spent recording acceleration over days and weeks increases due to animals engaging in a wider range of behaviours or experiencing greater variability in environmental conditions. This may mean that ODBA/VeDBA are best applied to individual activities, rather than to a full range of activities displayed while foraging as suggested by Skinner *et al.* (2014).

Defining and quantifying the behaviours that make up time-activity budgets are important steps in understanding the energetics of free-ranging marine mammals. Studies have attempted to determine time-activity budgets using a mix of acceleration, geolocation, altitude and depth data to visually discriminate behaviours (Yoda *et al.* 2001; Gomez-Laich *et al.* 2008; Insley 2008), or have used supervised or unsupervised classification techniques such as K-mean clustering techniques (Sakamoto *et al.* 2009), K-nearest neighbour algorithms (Bidder *et al.* 2014) or decision-tree classifications (Nathan *et al.* 2012). Activities can be linked to specific energy expenditures within a global framework (Elliott *et al.* 2013; Gomez-Laich *et al.* 2013; Wright *et al.* 2014), but are highly species, environment and activity specific. There is, thus, a need to link time-activity budgets to specific activity-related energy expenditure in free-ranging animals to better understand the relationships between individuals, their energetics and the environment.

Consequently, our first goal was to determine whether acceleration-based parameters could accurately predict the energy expended (independently assessed by doubly labelled water measurements of field metabolism) by two species of marine mammals, the northern and the Antarctic fur seals (*Callorhinus ursinus* and *Arctocephalus gazella*), in free-ranging conditions during individual foraging trips. Secondly, we investigated whether better estimates of energy expenditure could be obtained by considering time-activity budgets and breaking the foraging trips into behavioural activity components. Given that acceleration-based

predictors of energy expenditure are activity-specific and the importance of time-activity budgets on energy expenditure of free-ranging animals, we hypothesized that acceleration will better predict energy expenditure of fur seals foraging at sea when their individual time-activity budget is taken into account.

Materials and methods

DATA COLLECTION

Data were collected from 20 lactating northern fur seals (NFS) at the Reef rookery on St Paul Island (Bering Sea, 57°6′N–170°17′W) during the breeding season from August to September 2011 and from 20 lactating Antarctic fur seal (AFS) at Pointe Suzanne, Kerguelen Island (Southern Ocean, 49°26′S–70°26′E) during the breeding season from January to February 2012. All females were captured using a hoop net and were mature adults with a confirmed suckling pup. The females were carried over a short distance to a restraint board where they were anaesthetized with isoflurane gas. Standard morphometric measurements of length and axial girth were made to the nearest 0·5 cm, and mass was recorded using scale at ±0·2 kg.

Data loggers were glued to the dorsal mid-line fur using a two-part Devcon 5-min epoxy glue. Daily diary tags (DD, Wildlife Computers, Redmond, WA, USA) recording tri-axial acceleration at 16 Hz and depth, light level and water temperature at 1 Hz were glued as close as possible to the projection of the centre of mass on the back of the animal (roughly between the scapulae). Fastloc® GPS MK10 loggers (Wildlife Computers) were glued lower down the back from the DD tags. They recorded GPS coordinates along the track of the animal at sea, as well as depth and water temperature at 1 Hz. Once the devices were securely attached and the measure of energy expenditure via DLW was completed, the females were released upon full recovery from the anaesthesia and allowed to rejoin the colony. Individuals were recaptured after a single foraging trip at sea and anaesthetized as previously described, and all the data loggers were removed by cutting the fur beneath them. A second set of morphometric measurements was also taken at this time.

DIVING AND FORAGING BEHAVIOURS

We used depth data recorded by the DD or MK10 tags to determine diving behaviours using a custom-made R programme previously developed for Antarctic fur seals. Dives were defined as periods of time that animals spent under water below a minimum depth of 3 m and for a minimum of 4 s until they went back to the surface. Any drift in the pressure sensors or error spikes were corrected prior to analyses. Distances travelled at the surface of the ocean (horizontal distances) were calculated by measuring the linear distance between two successive GPS locations taking into account the curvature of the Earth using the Haversine formula (Sinnott 1984). GPS locations have a high spatial and temporal resolution (they were set to record a location every 5 min), so GPS tracks did not require interpolation or filtering (Tremblay *et al.* 2006). Part of the distance travelled under water while diving is inherently taken into account in the measured horizontal distance travelled. We calculated vertical distance travelled while diving by doubling the maximum dive depth of each dive.

Fur seal behaviours were separated into four categories to determine time-activity budgets: (i) diving; (ii) resting and sleeping; (iii) surface activities, grooming and slow travel; and (iv) fast transiting. These four behaviours were identified using a custom-made classification-tree algorithm in R detailed in Jeanniard-du-Dot

et al. (in press). In short, *Diving* and foraging time was defined as the period when animals were actively diving and included the post-dive intervals calculated using the package diveMove in R (https://cran.r-project.org/web/packages/diveMove/diveMove.pdf), validated for diving fur seals (Luque & Guinet 2007). *Resting* time was defined as the time when the running variance over 3 s on the raw acceleration signal was less than 2·5 m s^{-2} for all three axes for more than 5 min. *Transiting* time was the period during which the animals were neither diving nor resting and were moving at the surface at or faster than 1 m s^{-1} (calculated from GPS locations at specific times). Finally, s*urface activities,* grooming and slow travel time occurred when the animals were neither diving nor resting and were moving at the surface at a speed <1 m s^{-1}. Gaps in acceleration due to DD tags malfunction for northern fur seals were also quantified, and accuracy of the classification-tree model was visually verified over the entire foraging trip for all animals.

TOTAL AND ACTIVITY-SPECIFIC ENERGY EXPENDITURE

Measurements of field metabolic rates (MJ day^{-1}) were performed intravenously using the doubly labelled water (DLW) method (Lifson & McClintock 1966; Butler *et al.* 2004) while animals were under anaesthesia. We used a two-pool model and a plateau method from Speakman, Nair & Goran (1993) and converted CO_2 production rates into daily energy expenditure using a respiratory quotient RQ of 0·80 (Sparling *et al.* 2008; Dalton, Rosen & Trites 2014). More detailed information on DLW methods and procedures used are contained in Jeanniard-du-Dot *et al.* (in press). Energy spent during time on land was subtracted from total energy expenditure to obtain energy expenditure at sea only using previously determined values for females lactating while on land in northern (4·67 W kg^{-1} in Gentry & Kooyman 1986) and Antarctic fur seals (4·56 W kg^{-1} in Costa & Trillmich 1988).

The energy each animal spent performing each type of activity was determined using the activity-specific metabolic rates for northern and Antarctic fur seals as calculated by Jeanniard-du-Dot *et al.* (in press). In brief, we used the diving metabolic rate of 30·84 MJ day^{-1}, the transiting metabolic rate of 18·5 MJ day^{-1} and surface movements metabolic rate of 14·47 MJ day^{-1}. We multiplied these rates by the amount of time each individual spent engaged in their respective activities (in days) to obtain the energy expenditure per activity (in MJ). We did not include sleeping time in these analyses because the parameter estimates for this activity were not significant in the model results (Table 1 in Jeanniard-du-Dot *et al.* in press).

DYNAMIC BODY ACCELERATION

Vectorial Dynamic Body Acceleration (VeDBA, McGregor *et al.* 2009) was calculated using the tri-axial acceleration data collected at 16 Hz by the DD tag on the back of the animals. We performed the same analyses on both Overall Dynamic Body Acceleration (ODBA, Wilson *et al.* 2006) and VeDBA metrics, but only report VeDBA, which was slightly, but not significantly, more accurate in our analyses (Jeanniard-du-Dot 2015). The three axes, X (surge), Y (sway) and Z (heave), were first individually normalized using static data collected on all azimuths while the tags were still on a hard surface. The normalized signal was then filtered using a running mean of 2 s (Shepard *et al.* 2008; Fahlman *et al.* 2013; Dalton, Rosen & Trites 2014) to dissociate the static acceleration (due to the positioning of the animal in space in respect to gravity) from the dynamic acceleration (X_{dyn}, Y_{dyn} and Z_{dyn}, due to the movement of the animal). VeDBA was then calculated as follows:

Table 1. Proportion of total time at sea and average VeDBA spent in four types of activity for 16 lactating northern fur seal and 17 lactating Antarctic fur seal during a single foraging trip. Activities included active foraging (diving + post-dive surfacing), resting at the surface, transiting at a speed >1 m s^{-1} and slow surface movements (<1 m s^{-1})/grooming. Gap refers to the proportion of time when data were missing and could not be allocated to either of the four activity types. Values are means ± SE and asterisks show the values significantly different between species

Activity type	Proportion of at-sea time in each activity (%)		Average VeDBA during each type of activity (m s^{-2} kg^{-1})	
	NFS	AFS	NFS	AFS
Diving	28·6 ± 2·0 (20·5–47·8)	29·0 ± 0·7 (23·7–34·5)	0·0077 ± 0·0003*	0·0105 ± 0·0004*
Transiting	30·5 ± 1·8 (17·5–46·6)	26·4 ± 1·6 (15·3–36·9)	0·0109 ± 0·0004*	0·0179 ± 0·0011*
Surf. mov.	28·8 ± 1·4* (19·4–36·4)	36·3 ± 2·0* (24·9–47·7)	0·0119 ± 0·0007*	0·0198 ± 0·0009*
Resting	10·9 ± 1·3 (3·9–24·6)	8·2 ± 1·7 (1–16·9)	0·0033 ± 0·0001*	0·0049 ± 0·0002*
Gap	1·1 ± 0·26 (0·0–3·9)	NA	NA	NA

$$VeDBA = \sqrt{X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2}$$

We used the same equation to calculate VeDBA for specific types of activities, but only for acceleration displayed during the times animals where either diving (VeDBA$_D$), transiting (VeDBA$_T$), resting (VeDBA$_R$) or performing slow surface movements (VeDBA$_S$) based on the results from the time-activity budget analyses. Due to device malfunction, 19 of the 20 NFS DD tags had random periods of data collection interruptions during their deployments (from 0·3 to 3·9% of the data sets) that we accounted for in the calculation of VeDBA by substituting average overall acceleration to the times when no data were recorded.

STATISTICAL ANALYSES

Foraging parameters

Statistical differences between two groups (e.g. between species, or between two activity types) were tested with two-sample *t*-tests (α = 0·05) or Mann–Whitney *U*-tests depending on normality. Averages for dive parameters, such as for dive depths and dive durations, are nested within animals and were calculated using linear mixed-effect models with no fixed effects (only the intercept is calculated) and with individual as a random effect to take into account that each animal performed a different number of dives.

Energy expenditure vs. VeDBA

We tested whether VeDBA could reliably predict total energy expenditure at sea in fur seals using general linear models (lm, 'stats' package, R 3.0.3) or general linear model using generalized least square that allows for unequal variances (gls, 'nlme' package, R 3.0.3) after verifying models assumptions. Metabolic rate and VeDBA were mass corrected for each animal as both of these parameters are known to depend on the mass of the animals (Kleiber 1947; Gleiss, Wilson & Shepard 2011). The same types of analyses were performed between activity-specific energy expenditure and VeDBA (Diving, Transiting, and Surface movement). Finally, we compared estimated total energy expenditure from the best models to DLW measurements to determine the accuracy of different method. All results are means ± SE.

Results

Three DD tags failed to record any data and four stopped recording before the end of the foraging trip. Seven females

also came back on land with blood H and O isotopic levels too close to initial background levels to yield accurate metabolic rate measurements and were removed from further analyses. Consequently, sample size for analyses that only required acceleration data or that only required energy expenditure data was *n* = 16 for NFS and *n* = 17 for AFS. However, females missing acceleration data were usually not the ones also missing metabolic rate measurements. Consequently, sample size for analyses in which energy expenditure and acceleration data were combined was *n* = 12 for northern and *n* = 13 for Antarctic fur seals

DIVING AND FORAGING BEHAVIOURS

The female northern fur seals weighed on average 37·9 ± 1·3 kg (30·8–55·6 kg) prior to departure and female Antarctic fur seals weighed 31·0 ± 0·8 kg (25–39 kg). Foraging trips lasted 7·96 ± 2·17 days (4·26–12·03 days) over 750 ± 50 km (391–1200 km) for NFS, and 7·65 ± 3·88 days (2·34–15·47 days) and 635 ± 77 km (225–1295 km) for AFS (both *P* > 0·221). Both species of fur seals spent similar amount of time diving (~29%, *P* = 0·328) and transiting fast at the surface (26–30%, *P* = 0·063, Table 1). They also spent ~ 1/3 of their time performing slow movements at the surface (28–36%), but Antarctic fur seals spent slightly more time doing so than northern fur seals (*P* = 0·013). Conversely, both species spent the smallest proportion of their time resting and sleeping at the surface (~ 8–10%, *P* = 0·401).

TOTAL ENERGY EXPENDITURE VS. VEDBA

Energy expenditure while foraging at sea were not significantly different in northern and Antarctic fur seals (155·10 ± 13·01 MJ for NFS and 121·41 ± 17·06 MJ for AFS, *P* > 0·09). The same was true for energy expenditures per day whether for the total DLW time (20·02 ± 1·27 MJ day^{-1} for NFS and 17·02 ± 1·08 MJ day^{-1} for AFS, *P* = 0·082) or for the at-sea time only (20·93 ± 1·47 MJ day^{-1} for NFS and 17·72 ± 1·15 MJ day^{-1} for AFS, *P* = 0·097). Averaging dynamic body acceleration over the entire foraging trip (and for each

type of activity, see below and in Table 1) showed that total average VeDBA was overall greater for AFS (0.411 ± 0.02 m s^{-2} or 0.013 ± 0.001 m s^{-2} kg^{-1}) than for NFS (0.312 ± 0.014 m s^{-2} or 0.008 ± 0.0005 m s^{-2} kg^{-1}, $P < 0.0004$). Average VeDBA over the entire foraging trip only explained ~ 36% of variability in energy expenditure at sea ($R^2 = 0.36$, Fig. 1a). Rate of energy expenditure (in MJ day^{-1}) is not accurately predicted by acceleration (Fig. 1b, $R^2 = 0.15$). Similar trends were observed for similar analyses when parameters were not mass standardized, but accuracy was overall lower [$R^2 = 0.30$ for EE (MJ) vs. VeDBA (m s^{-2}) and $R^2 = 0.08$ for EE (MJ day^{-1} vs. VeDBA (m s^{-2})].

ACTIVITY-SPECIFIC ENERGY EXPENDITURE VS. ACTIVITY-SPECIFIC VEDBA

When split by activity, VeDBA was the greatest when the animals were either transiting (0.414 ± 0.013 m s^{-2} for

NFS and 0.556 ± 0.026 m s^{-2} for AFS, $P < 0.05$) or active at the surface of the water (0.456 ± 0.22 m s^{-2} for NFS and 0.605 ± 0.017 m s^{-2} for AFS, $P < 0.05$). VeDBA while diving was significantly lower than VeDBA for any other activity (0.297 ± 0.013 m s^{-2} for NFS and 0.310 ± 0.018 m s^{-2} for AFS, $P < 10^{-6}$, no difference between species $P > 0.05$, see Table 1). When animals were resting and sleeping at the surface, VeDBA was the lowest, but was still significantly >0 for both species ($P < 10^{-16}$), which suggests there was significant residual dynamic acceleration due to external factors (waves, etc.) when the seals were lying on the water surface (quantification and analyses of these factors can be found in Jeanniard-du-Dot 2015).

Energy spent performing each type of activity (MJ kg^{-1}) was significantly related to activity-specific VeDBA when standardized for time spent performing activities (m s^{-2} kg^{-1} × day, Fig. 2). VeDBA/EE relationships improved greatly when split by type of activity rather than over the full foraging trip (all $R^2 > 0.85$). Both species had similar mechanic-to-energy (VeDBA/EE) efficiencies while diving, but differences in slopes indicate that they differed while transiting or during surface activity. Regression slopes are lower during transiting and surface activity than
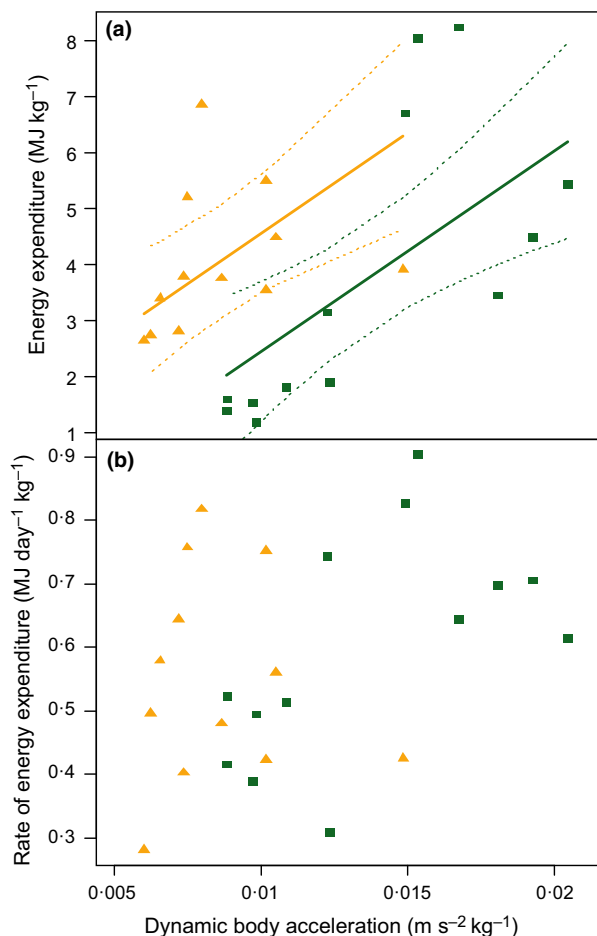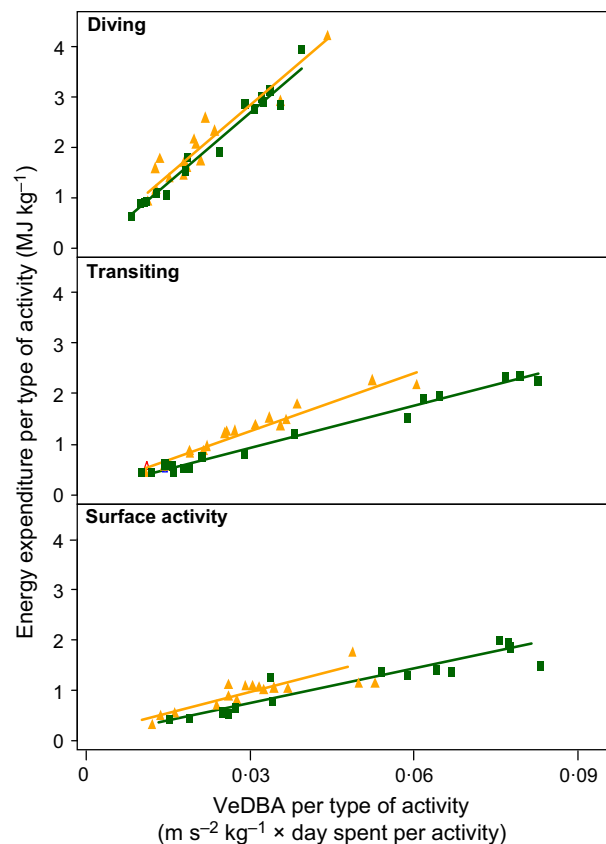

Fig. 1. Relationships for northern fur seals (yellow triangles) and Antarctic fur seals (green squares) between energy expenditure in MJ kg^{-1} (a) or rate of energy expenditure in MJ day^{-1} kg^{-1} (b) and the average dynamic body acceleration over the entire foraging trip in m s^{-2} kg^{-1}. Each data point represents a single animal and was mass corrected. Panel a: $R^2 = 0.36$, AIC = 102.1, slope $P = 0.002$, species $P = 0.02$. Panel b: there were no significant species-specific relationships between VeDBA and the rate of energy expenditure.

Fig. 2. Relationships between activity-specific VeDBA standardized for individual time-activity budgets and body mass and activity-specific energy expenditure in MJ kg^{-1} for lactating northern fur seals (triangle symbols, $n = 16$) and Antarctic fur seals (square symbols $n = 17$). Plain lines show the results of linear models that included species as an independent variable.

while diving. Specific equations for diving, transiting and surface activity from Fig. 2 included the following:

$$EE_{Dive}(MJ\ kg^{-1}) \sim (0{\cdot}10 \pm 0{\cdot}10) + (91{\cdot}99 \pm 4{\cdot}42)$$
$$\times VeDBA_{Dive}(m\ s^{-2}kg^{-1} * day) + (0{\cdot}14 \pm 0{\cdot}08$$
$$for\ NFS\ only); R^2 = 0{\cdot}94, slope\ P < 2{\cdot}10^{-16}$$

$$\text{eqn 1}$$

$$EE_{Transit}(MJ\ kg^{-1}) \sim (0{\cdot}14 \pm 0{\cdot}05) + (27{\cdot}62 \pm 1{\cdot}11)$$
$$\times VeDBA_{Transit}(m\ s^{-2}kg^{-1} * day) + [(0{\cdot}06 \pm 0{\cdot}08)$$
$$+ (10{\cdot}19 \pm 2{\cdot}54) \times VeDBA_{Transit}for\ NFS\ only];$$
$$R^2 = 0{\cdot}96, slope\ P < 2{\cdot}10^{-16}$$

$$\text{eqn 2}$$

$$EE_{Surf}(MJ\ kg^{-1}) \sim (0{\cdot}06 \pm 0{\cdot}07) + (23{\cdot}40 \pm 1{\cdot}48)$$
$$\times VeDBA_{Surf}(m\ s^{-2}kg^{-1} * day) + [(0{\cdot}22 \pm 0{\cdot}06)$$
$$\times VeDBA_{Surf}\ for\ NFS\ only]; R^2$$
$$= 0{\cdot}90, slope\ P < 2{\cdot}10^{-15}$$

$$\text{eqn 3}$$

Similar analyses with parameters that were not mass standardized were once again not as accurate as the mass standardized ones above, but all R^2 were still above 0·89.

PREDICTING TOTAL ENERGY EXPENDITURE AT SEA FROM ACTIVITY-SPECIFIC VEDBA

Total energy expenditure can best be predicted by combining the predicted activity-specific energy expenditures EE_{Dive}, $EE_{Transit}$ and EE_{Surf} obtained from Eqs. 1, 2 and 3 using activity-specific VeDBA and time-activity budgets:

$$\text{Total } EE_{Pred.} \sim EE_{Dive} + EE_{Transit} + EE_{Surf} \qquad \text{eqn 4}$$

Total energy expenditure estimated from eqn 4 correlated well with measured total energy expenditure from the DLW method ($R^2 = 0{\cdot}70$, Fig. 3). There was no systematic differences between observed and simulated values (slope of the linear regression not significantly different from 1 ($1{\cdot}00 \pm 0{\cdot}14$, $P < 4{\cdot}10^{-7}$) and intercept not significantly different from 0 ($1{\cdot}10^{-15} \pm 0{\cdot}56$, $P = 1$), so our model yielded appropriate estimates of total energy expenditure.

Discussion

We collected data on more than 25 animals in free-ranging conditions and used acceleration and other foraging-related parameters paired with measures of field energy expenditure to test whether acceleration metrics are accurate predictors of metabolic rates at sea in wild top marine predators. Our acceleration data allowed us to analyse time-activity budgets of individual fur seals in the wild at a much finer scale than usual methods based on location and dive data only. Our results showed that VeDBA
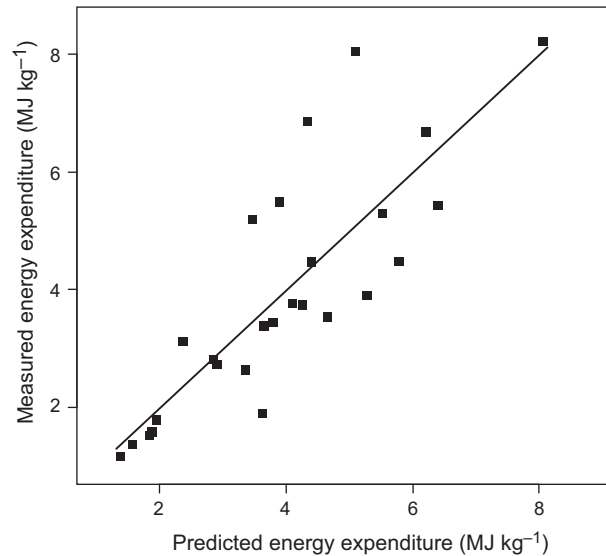

Fig. 3. Comparison between measured energy spent at sea by lactating northern and Antarctic fur seals using the DLW method and the predicted energy expenditure estimated from Jeanniard-du-Dot *et al*. (in press). The regression line has an intercept of $1{\cdot}4 \times 10^{-15} \pm 0{\cdot}56$, not statistically different from 0, and a slope of $1{\cdot}00 \pm 0{\cdot}13$, not statistically different from 1, $R^2 = 0{\cdot}70$.

calculated independently of foraging behaviours or time-activity budgets could not accurately estimate energy expenditure of full foraging trips. However, activity-specific acceleration metrics could accurately predict energy spent during specific types of behaviours at sea and could be summed by types of activity (i.e. diving, transiting, surface activity and resting) to accurately estimate energy expenditure of complete foraging trips.

DYNAMIC BODY ACCELERATION AS A PREDICTOR OF ENERGY EXPENDITURE DURING A FULL FORAGING TRIP

Our results show that average VeDBA over a full trip is not an accurate predictor of energy expenditure and could only explain 36% of its variation (Fig. 1a). This R^2 is lower than values reported for other vertebrates measured in captivity/semi-captivity (0·47 for diving Steller sea lions, Fahlman *et al*. 2008; 0·84 in birds, Halsey *et al*. 2009a; 0·60 for swimming sharks, Gleiss *et al*. 2010; 0·56 for turtles, Halsey *et al*. 2011). The poor ability of VeDBA to predict energy expenditure over a full trip is likely related to the assumptions behind VeDBA as a proxy for energy expenditure and/or in the sources of unmeasured error associated with free-ranging environmental conditions (Gleiss, Wilson & Shepard 2011; Halsey, Shepard & Wilson 2011).

First, most studies have validated VeDBA in captive or semi-captive settings, that is in controlled conditions (Wilson *et al*. 2006; Gleiss *et al*. 2010; Halsey *et al*. 2011; Fahlman *et al*. 2013). However, free-ranging marine animals live in a dense medium under fluid environmental

conditions and seals spend a significant portion of their time at the water surface, where wind-related motions, mainly through wave action can interfere with energy expenditure and the dynamic body acceleration signal. This residual 'environmental' acceleration largely disappears when the animals dive and is consistent between seals over their foraging trips. It can thus be corrected, but it still impacts the slope of the VeDBA/EE relationships (Jeanniard-du-Dot 2015). Another difference between other validation studies and ours is the variation in the duration of measurements taken (i.e. hours vs. days or weeks). In our case, the northern and Antarctic fur seals undertook foraging trips that averaged 7–8 days (range 2·5–15 days). A fur seals that makes a long foraging trip is likely to allocate energy differently compared to an animal that makes a short trip, yet averaging VeDBA over time does not account for such differences. We suspect this is why none of our analyses that used metabolic rate as our reference measurement (in MJ day^{-1}, Fig. 1b) yielded significant relationships with VeDBA, unlike in other studies.

Secondly, energy expended by our fur seals could have been affected by physiological sources of errors that had no effect on VeDBA – or vice versa. For example, thermoregulation or digestion costs, growth and gestation can affect energy expenditure, but are independent of VeDBA (Rosen & Trites 1997; Costa & Williams 1999; Green *et al.* 2009). However, the impact of these factors might be minimal if animals have high locomotion costs and operate close to their metabolic ceilings (Costa 2007). Another factor is body condition of seals that affects buoyancy, which in turn affects mechanical power and cost of transportation (through changes in buoyancy and gliding – Williams *et al.* 2000; Wilson *et al.* 2010). In addition, fur seals typically transit by porpoising at the surface, which means that they switch from moving through air to moving through water in a matter of seconds. Such changes in movement between mediums with highly different densities likely affect VeDBA in different ways, as would differences in gaits between swimming and porpoising movements. Collectively, such studies point to an uncoupling between a significant portion of metabolic rate and the acceleration which could potentially contribute to the uncertainty in the VeDBA and energy expenditure relationship (Halsey, Shepard & Wilson 2011).

In addition to the uncertainties associated with VeDBA discussed above, there are also inherent uncertainties with using the doubly labelled water method (DLW) as our reference measure of energy expenditure that might affect accuracy of our EE/VeDBA relationship. Some studies of specialist marine carnivores have suggested that the DLW method has high accuracy, but low precision (Speakman 1993). For example, the DLW method applied to grey seals (*Halichoerus grypus*) subjected to simulated foraging conditions over 5-day periods yielded estimates of energy expenditure for groups averages that were similar to estimates derived from respirometry (group error was 0·5%, Sparling *et al.* 2008), but individual error was ~ ±

40%. Similarly, a study on captive northern fur seals showed that the average error of the DLW method compared to respirometry measurements could be as low as ~ 0·8% but as high as ~ 27% depending on the calculation method used and the time of year (lowest in the fall and highest in the summer, Dalton, Rosen & Trites 2014). Consequently, the error associated with our reference measurement of energy expenditure is likely significant since we compared DLW to VeDBA measurements at the individual level (one DLW and one VeDBA point per animal). We recognize that using DLW measurements as a reference measurement of energy expenditure comes with associated caveats, but was the only option available to us to study energy expenditure at sea for free-ranging fur seals.

Either way, there seems to be no escaping the fact that VeDBA metrics are not an appropriate means to predict the total energy expended regardless of method used to establish the reference energy expenditure, especially when measured over long periods of time in the wild when animals engage in different behaviours that have markedly different energetic costs (Green *et al.* 2009; Halsey, Shepard & Wilson 2011; Dalton, Rosen & Trites 2014). A study of free-ranging thick-billed murres (*Uria lomvia*), for example, found that activity-specific VeDBAs were better predictors of energy expenditure during a foraging trip than overall VeDBA, especially if one activity type had a greater energetic cost than others (in this case flying, Elliott *et al.* 2013). Animals are known to incur different energetic costs to undertake different activities, and different relationships are known to exist between VeDBA and EE depending on gaits in humans (Halsey *et al.* 2008), intensities of swimming in sharks (Gleiss, Gruber & Wilson 2009) and types of muscles involved in the movement of birds (Gomez-Laich *et al.* 2008). All told, this suggests that the poor ability of total VeDBA to predict the energetic cost of foraging trips undertaken by our fur seals might be due to differences in time-activity budgets (i.e. how the animals partitioned their time at sea between diving, transiting, resting and surface activities).

TIME-ACTIVITY BUDGETS AND ACTIVITY-SPECIFIC ENERGY EXPENDITURES

Time budgets are the currency that define foraging strategies and ultimately reflect the foraging efficiencies of animals when combined with energetics. Our results show that VeDBA is much more accurate at predicting energy expend by fur seals at the activity level rather than over a full trip. It also shows that VeDBA needs to be broken down by type of activity and summed together to predict total energy expenditure. The high correlations between our calculated activity-specific energy expenditures and the activity-specific VeDBAs (all $R^2 > 0.85$) gives confidence that VeDBA is a much better proxy for energy expenditure when broken down by activity type. This is because the mechanical to energy efficiency or slopes of the VeDBA/EE relationships vary by activity type.

Changes in VeDBA affect mechanical power and thus energy expenditure more drastically while diving than while transiting or during surface activities (Fig. 2). This means that small changes in measures of VeDBA can lead to larger changes in estimates of diving energy expenditure than of energy spent in surface behaviours. Why diving has inherently the lowest VeDBA but the highest costs compared to other activities is likely due to the fact that animals have to compromise between high speeds to maximize time foraging at depth and drag that increases with swimming velocity (Costa & Williams 1999). In comparison, transiting also involves high speed swimming, but it is usually done either at depths where drag is the lowest (i.e. at three body diameter depth, Williams 1989; Hindle, Rosen & Trites 2010), or by porpoising which increases locomotion efficiency (Boyd 2002). Slow surface movements also occur at the surface where drag is high, but movements are at lower velocity when drag is decreased (Costa & Williams 1999).

Differences in EE/VeDBA relationships were also observed in marine birds between flying and all other activities they engage in (i.e. resting at sea surface, diving and walking, Gomez-Laich *et al.* 2011; Elliott *et al.* 2013). These differences were attributed to the medium (air or water) in which the animal moved and to the mechanics and the types of muscles involved in each activity (i.e. the force production to movement relationship of muscles and their contractile properties). In the case of fur seals, it is unlikely that type of muscle involved would make a difference as they use fore flipper propulsion for locomotion at sea, but the medium in which animal evolves is likely a major factor. Indeed, densities of air and water differ by a factor of ~800, which undoubtedly affects VeDBA differently than it affects energy expenditure (especially from a deceleration when re-entering water during porpoising).

As mentioned earlier, DLW is known to lack precision at the individual level but to provide estimates of energy expenditure with a reasonable accuracy at the group or population level (Speakman 1993). Unlike full foraging trip models in which individual DLW measurements were compared to overall acceleration, activity-specific models compared activity-specific acceleration to the energy that each animal spent per activity (in MJ) calculated using parameter estimates of eq. 2 from Jeanniard-du-Dot *et al.* (in press). These parameter estimates provide average metabolic rates per activity (in MJ day^{-1}) over all study animals, that is at the group level. Consequently, using 'group' metabolic rates in the activity-specific models might improve accuracy of predictions for total energy expenditure by reducing the individual errors associated with DLW measurements. This means that ~20–35% of the uncertainty in the global model could be attributed to errors in the DLW measurements and individual variability in time-activity budgets and foraging strategies (even if it was impossible to tease apart the respective effects of these two parameters).

Our findings indicate that energy expenditure by fur seals over full foraging trips can be accurately determined from body acceleration, but only if it is done using activity-specific time budgets. The predicted energy expenditure of our study animals derived from activity-specific measures of body movement (i.e. VeDBA × activity budget) corresponded well with the DLW measured energy expenditures (Fig. 3, $R^2 = 0.71$). Yet, accuracy of the general model (eqn 4) is not as strong as the one for activity-specific models (see Fig. 2). This is likely due to the fact that energy spent during resting time was not taken into account in the calculation of predicted energy expenditure. The other contributing factor that likely impacted the relationship in Fig. 3 is the previously mentioned error associated with the measured total energy expenditure from the DLW method. The individual error was determined for measured DLW values, but was likely buffered for the predicted values because it was calculated using 'population' estimates from the models.

Earlier methods to estimate energy expenditure at sea were based solely on dive profiles form TDR records (Arnould, Boyd & Speakman 1996). Interestingly, we did not find the same negative relationship between metabolic rate and dive rate in our animals ($R^2 = 0.03$). This might be either to their low sample size ($n = 9$) or to the crudeness of their behavioural data (depth recorded every 10 s only, while average dive duration can be as short at 18 s depending on animals – average for AFS 50 ± 23 s). In any case, they only took into account proportion of time spent involved in one activity (although the most expensive one), which is insufficient to accurately determine energy expenditure at sea in fur seals.

In a finer scale study, Skinner *et al.* (2014) also found that VeDBA multiplied by distance travelled, mass of the animal and vertical distance swam was together the best metrics to assess energy expenditure of northern fur seals at sea. We applied the best model from Skinner *et al.* (2014) to our data and only obtained an $R^2 = 0.50$. However, there are parallels in our two respective models in that both take into account effort and time spent diving vs. other activities (see Table 2.4 in Jeanniard-du-Dot 2015). Both models point out that knowing how much time an animal spends foraging, diving, transiting and being surface active is as important as knowing the intensity with which the seals perform these activities.

Conclusions

All in all, our results show that the time an animal decides to allocate to activities that have different metabolic rates is important for obtaining accurate estimates of energetic costs of foraging. Estimates of total energy expended by fur seals should thus be done using the activity-specific DBA paired with time-activity budget (i.e. eqn 4). It also emphasizes the potential for acceleration to determine behavioural activity budgets and energy expenditures under wild conditions and over a wide range of activities

at a much finer scale than more traditional location and depth loggers and at temporal and spatial scales that are relevant to ecological studies. In any case, being able to accurately calculate foraging costs helps to better understand the energetic requirements of free-ranging seals and other marine mammals, and whether they can be met in the wild. Knowing foraging costs also contributes to assessing the ecological impacts that marine mammals have on trophic webs, and how changes in time-activity budgets due to environmental changes affect their fitness. Such knowledge is particularly important for the conservation and management of species that are easily impacted by ecosystem shifts and environmental changes, especially for fur seals that are already performing close to their metabolic ceilings, and may have limited scope to adapt to coming climate changes.

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Data accessibility

Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n8s3c (Jeanniard-du-Dot *et al.* 2016).

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