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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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25 Running headline: activity-specific acceleration predicts energy expenditure

26 Keywords: Acceleration; VeDBA, Time-activity budget, northern fur seal, Antarctic fur seal,
27 energy expenditure, metabolic rate, foraging

28

29 **Abstract**

30 1- Energy expenditure is an important component of foraging ecology, but is extremely
31 difficult to estimate in free-ranging animals and depends on how animals partition their
32 time between different activities during foraging. Acceleration data has emerged as a new
33 way to determine energy expenditure at a fine scale but needs to be tested and validated
34 in wild animals.

35 2- This study investigated whether vectorial dynamic body acceleration (VeDBA) could
36 accurately predict the energy expended by marine predators during a full foraging trip.
37 We also aimed to determine whether the accuracy of predictions of energy expenditure
38 derived from acceleration increased when partitioned by different types of at-sea
39 activities (i.e., diving, transiting, resting and surface activities) vs calculated activity-
40 specific metabolic rates.

41 3- To do so, we equipped 20 lactating northern (*Callorhinus ursinus*) and 20 Antarctic fur
42 seals (*Arctocephalus gazella*) with GPS, time-depth recorders and tri-axial
43 accelerometers, and obtained estimates of field metabolic rates using the doubly-labelled
44 water (DLW) method. VeDBA was derived from tri-axial acceleration, and at-sea
45 activities (diving, transiting, resting and surface activities) were determined using dive
46 depth, tri-axial acceleration and traveling speed.

47 4- We found that VeDBA did not accurately predict the total energy expended by fur seals
48 during their full foraging trips ($R^2 = 0.36$). However, the accuracy of VeDBA as a
49 predictor of total energy expenditure increased significantly when foraging trips were
50 partitioned by activity and used activity-specific VeDBA paired with time activity
51 budgets ($R^2 = 0.70$). Activity-specific VeDBA also accurately predicted the energy
52 expenditures of each activity independent of each other ($R^2 > 0.85$).

53 5- Our study confirms that acceleration is a promising way to estimate energy expenditures
54 of free-ranging marine mammals at a fine scale never attained before. However, it shows
55 that it needs to be based on the time-activity budget that make up foraging trips rather
56 than being derived as a single measure of VeDBA applied to entire foraging trips. Our
57 activity-based method provides a cost-effective means to accurately calculate energy
58 expenditures of fur seals using acceleration and time-activity budgets, a stepping stone
59 for numerous other research fields.

60 **Introduction**

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

70 Heart rate monitors, accelerometers, and doubly-labelled water (DLW) have all been
71 used to measure energy expenditure in vertebrates (Lifson & McClintock 1966; Butler *et al.*
72 1992; Butler 1993; Speakman 1997; Froget *et al.* 2004; Wilson *et al.* 2006; Young *et al.* 2011).
73 However, heart rates and DLW measurements can be invasive, very costly, have their own
74 biological limitations, and are often impractical for large wild animals (Nagy 1980; Thorarensen,
75 Gallagher & Farrell 1996; Ward *et al.* 2002; Butler *et al.* 2004; Dalton, Rosen & Trites 2014).
76 In addition, these techniques are not readily applicable to large sample sizes or across the
77 different temporal scales that are required in many ecological studies. More recently,
78 accelerometry techniques have emerged in the field of ecological energetics and have the
79 potential to provide valuable fine-scale information over days, weeks or months. This is why
80 simple measures of body movement from accelerometry are increasingly being sought to
81 estimate energy expended by animals

82 The Overall Dynamic Body Acceleration (ODBA) and Vectorial Dynamic Body
83 Acceleration (VeDBA) are two very similar tri-axial body acceleration metrics that can be linked
84 to energy expenditure (Wilson *et al.* 2006; Halsey *et al.* 2009a; Halsey *et al.* 2009b; Qasem *et al.*
85 2012). ODBA and VeDBA have been tested and calibrated on various taxa, whether marine or
86 terrestrial, endotherms or ectotherms during different types of activities (walking, flying,
87 swimming etc., Fahlman *et al.* 2008; Halsey *et al.* 2008; Gleiss, Gruber & Wilson 2009; Halsey
88 & White 2010; Gomez-Laich *et al.* 2011; Halsey *et al.* 2011). They appear to have acceptable
89 accuracy for determining energy expenditure, but relationships between acceleration and energy
90 expenditure vary by species and by type of activity, and need to be calibrated for each case
91 (Halsey *et al.* 2008; Elliott *et al.* 2013; Wright *et al.* 2014). They also need to be tested with free-
92 ranging animals undertaking their full-suite of natural activities under different environmental
93 conditions.

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

102 Most validation and calibration studies of ODBA/VeDBA have been conducted in
103 controlled environments over short periods, which might buffer the above limitations. For
104 example, ODBA correlates with energy expenditure of semi-captive Steller sea lions
105 (*Eumetopias jubatus*) trained to dive at sea (although with an R^2 of 0.47, Fahlman *et al.* 2008),
106 but does not correlate with the daily metabolic rate of captive northern fur seals over a 5-day
107 period (Dalton, Rosen & Trites 2014). This suggests that the predictive power of ODBA may
108 decrease as time spent recording acceleration over days and weeks increases due to animals
109 engaging in a wider range of behaviours or experiencing greater variability in environmental
110 conditions. This may mean that ODBA/VeDBA are best applied to individual activities, rather
111 than to a full range of activities displayed while foraging as suggested by Skinner *et al.* (2014).

112 Defining and quantifying the behaviours that make up time-activity budgets are an
113 important step in understanding the energetics of free-ranging marine mammals. Studies have
114 attempted to determine time-activity budgets using a mix of acceleration, geolocation, altitude
115 and depth data to visually discriminate behaviours (Yoda *et al.* 2001; Gomez-Laich *et al.* 2008;
116 Insley 2008), or have used supervised or unsupervised classification techniques such as K-mean
117 clustering techniques (Sakamoto *et al.* 2009), K-nearest neighbour algorithms (Bidder *et al.*
118 2014) or decision-tree classifications (Nathan *et al.* 2012). Activities can be linked to specific
119 energy expenditures within a global framework (Elliott *et al.* 2013; Gomez-Laich *et al.* 2013;
120 Wright *et al.* 2014), but are highly species-, environment- and activity-specific. There is, thus, a
121 need to link time-activity budgets to specific activity-related energy expenditure in free-ranging
122 animals to better understand the relationships between individuals, their energetics and the
123 environment.

124 Consequently, our first goal was to determine whether acceleration-based parameters
125 could accurately predict the energy expended (independently assessed by doubly-labelled water
126 measurements of field metabolism) by two species of marine mammals, the northern and the
127 Antarctic fur seals (*Callorhinus ursinus* and *Arctocephalus gazella*), in free-ranging conditions
128 during individual foraging trips. Second, we investigated whether better estimates of energy
129 expenditure could be obtained by considering time-activity budgets and breaking the foraging
130 trips into behavioural activity components. Given that acceleration-based predictors of energy
131 expenditure are activity-specific and the importance of time-activity budgets on energy
132 expenditure of free-ranging animals, we hypothesized that acceleration will better predict energy
133 expenditure of fur seals foraging at sea when their individual time-activity budget is taken into
134 account.

135 **Material and methods**

136 *Data collection*

137 Data were collected from 20 lactating northern fur seals (NFS) at the Reef rookery on St
138 Paul Island (Bering Sea, 57°6'N - 170°17'W) during the breeding season from Aug-Sep 2011,
139 and from 20 lactating Antarctic fur seal (AFS) at Pointe Suzanne, Kerguelen Island (Southern
140 Ocean, 49°26'S - 70°26'E) during the breeding season from Jan-Feb 2012. All females were

141 captured using a hoop net and were mature adults with a confirmed suckling pup. The females
142 were carried over a short distance to a restraint board where they were anaesthetized with
143 isoflurane gas. Standard morphometric measurements of length and axial girth were made to the
144 nearest 0.5 cm, and mass was recorded using scale at ± 0.2 kg.

145 Data loggers were glued to the dorsal mid-line fur using a 2-part Devcon 5 min epoxy
146 glue. Daily Diary tags (DD, Wildlife Computers) recording tri-axial acceleration and tri-axial
147 magnetic field at 16Hz, and depth, light level, and water temperature at 1 Hz were glued as close
148 as possible to the projection of the center of mass on the back of the animal (roughly between the
149 scapulae). Fastloc[®] GPS MK10 loggers (Wildlife Computers) were glued lower down the back
150 from the DD tags. They recorded GPS coordinates along the track of the animal at sea, as well as
151 depth and water temperature at 1 Hz. Once the devices were securely attached and the measure
152 of energy expenditure via DLW were completed, the females were released upon full recovery
153 from the anaesthesia and allowed to rejoin the colony. Individuals were recaptured after a single
154 foraging trip at sea and anaesthetized as previously described, and all the data loggers were
155 removed by cutting the fur beneath them. A second set of morphometric measurements was also
156 taken at this time.

157 *Diving and foraging behaviours*

158 We used depth data recorded by the DD or MK10 tags to determine diving behaviours
159 using a custom-made R program previously developed for Antarctic fur seals. Dives were
160 defined as periods of time that animals spent under water below a minimum depth of 3m and for a
161 minimum of 4 seconds until they went back to the surface. Any drift in the pressure sensors or error
162 spikes were corrected prior to analyses. Distances traveled at the surface of the ocean (horizontal
163 distances) were calculated by measuring the linear distance between two successive GPS
164 locations taking into account the curvature of the Earth using the Haversine formula (Sinnott
165 1984). GPS locations have a high spatial and temporal resolution (they were set to record a
166 location every 5 min), so GPS tracks did not require interpolation or filtering (Tremblay *et al.*
167 2006). Part of the distance traveled under water while diving is inherently taken into account in
168 the measured horizontal distance traveled. We calculated vertical distance traveled while diving
169 by doubling the maximum dive depth of each dive.

170 Fur seal behaviours were separated into 4 categories to determine time-activity budgets:
171 1) diving; 2) resting and sleeping; 3) surface activities, grooming, slow travel; and 4) fast
172 transiting. These 4 behaviours were identified using a custom-made classification-tree algorithm
173 in R detailed in Jeanniard du Dot *et al.* (In review). In short, *Diving* and foraging time was
174 defined as the period when animals were actively diving and included the post-dive intervals
175 calculated using the package *diveMove* in R (Author, S. Luque), validated for diving fur seals
176 (Luque & Guinet 2007). *Resting* time was defined as the time when the running variance over 3
177 sec on the raw acceleration signal was less than 2.5 m/s^2 for all 3 axes for more than 5 min.
178 *Transiting* time was the period during which the animals were neither diving nor resting, and
179 were moving at the surface at or faster than 1m/sec (calculated from GPS locations at specific
180 times). Finally, *surface activities*, grooming and slow travel time occurred when the animals
181 were neither diving nor resting, and were moving at the surface at a speed $< 1\text{m/sec}$. Gaps in
182 acceleration due to DD tags malfunction for northern fur seals were also quantified, and accuracy
183 of the classification-tree model was visually verified over the entire foraging trip for all animals.

184 *Total and activity-specific energy expenditure*

185 Measurements of field metabolic rates (MJ/day) were performed intravenously using the
186 Doubly-Labelled Water (DLW) method (Lifson & McClintock 1966; Butler *et al.* 2004) while
187 animals were under anesthesia. We used a two-pool model and a plateau method from
188 Speakman, Nair and Goran (1993), and converted CO_2 production rates into daily energy
189 expenditure using a respiratory quotient RQ of 0.80 (Sparling *et al.* 2008; Dalton, Rosen & Trites
190 2014). More detailed information on DLW methods and procedures used are contained in
191 Jeanniard du Dot *et al.* (In review). Energy spent during time on land was subtracted from total
192 energy expenditure to obtain energy expenditure at sea only using previously determined values
193 for females lactating while on land in northern (4.67 W/kg in Gentry & Kooyman 1986) and
194 Antarctic fur seals (4.56 W/kg in Costa & Trillmich 1988).

195 The energy each animal spent performing each type of activity was determined using the
196 activity-specific metabolic rates for northern and Antarctic fur seals as calculated by Jeanniard
197 du Dot *et al.* (In review). In brief, we used the diving metabolic rate of 30.84MJ/d, the transiting
198 metabolic rate of 18.5 MJ/d, and surface movements metabolic rate of 14.47 MJ/d. We
199 multiplied these rates by the amount of time each individual spent engaged in their respective

200 activities (in d) to obtain the energy expenditure per activity (in MJ). We did not include sleeping
201 time in these analyses because the parameter estimates for this activity were not significant in the
202 model results (Table 2 in Jeanniard du Dot *et al.* In review).

203 *Dynamic Body Acceleration*

204 Vectorial Dynamic Body Acceleration (McGregor *et al.* 2009) was calculated using the
205 tri-axial acceleration data collected at 16Hz by the DD tag on the back of the animals. We
206 performed the same analyses on both Overall Dynamic Body Acceleration (ODBA, Wilson *et al.*
207 2006) and VeDBA metrics, but only report VeDBA which was slightly, but not significantly,
208 more accurate in our analyses (Jeanniard du Dot 2015). The three axes, X (surge), Y (sway) and
209 Z (heave), were first individually normalized using static data collected on all azimuths while the
210 tags were still on a hard surface. The normalized signal was then filtered using a running mean of
211 2s (Shepard *et al.* 2008; Fahlman *et al.* 2013; Dalton, Rosen & Trites 2014) to dissociate the
212 static acceleration (due to the positioning of the animal in space in respect to gravity) from the
213 dynamic acceleration (X_{dyn} , Y_{dyn} and Z_{dyn} , due to the movement of the animal). VeDBA was then

214 calculated as:
$$VeDBA = \sqrt{X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2}$$

215 We used the same equation to calculate VeDBA for specific types of activities, but only
216 for acceleration displayed during the times animals were either diving (VeDBA_D), transiting
217 (VeDBA_T), resting (VeDBA_R) or performing slow surface movements (VeDBA_S) based on the
218 results from the time-activity budget analyses. Due to the device malfunction, the DD tags had
219 random periods of data collection interruptions in 19 out of the 20 NFS deployments (from 0.3 to
220 11.5 % of the datasets) that we accounted for in the calculation of VeDBA by substituting
221 average overall acceleration to the times when no data were recorded.

222 *Statistical analyses*

223 *Foraging parameters* – Statistical differences between 2 groups (for example between
224 species, or between 2 activity types) were tested with two-sample *t*-tests ($\alpha = 0.05$) or Mann-
225 Whitney tests depending on normality. Averages for dive parameters, such as for dive depths and
226 dive durations, are nested within animals and were calculated using linear mixed-effect models
227 with no fixed effects (only the intercept is calculated) and with individual as a random effect to
228 take into account that each animal performed a different number of dives.

229 *Energy expenditure versus VeDBA* – We tested whether VeDBA could reliably predict
230 total energy expenditure at sea in fur seals using general linear models (lm, ‘stats’ package, R
231 3.0.3) or general linear model using generalized least square that allows for unequal variances
232 (gls, ‘nlme’ package, R 3.0.3) after verifying models assumptions. Metabolic rate and VeDBA
233 were mass-corrected for each animal as both of these parameters are known to depend on the
234 mass of the animals (Kleiber 1947; Gleiss, Wilson & Shepard 2011). The same types of analyses
235 were performed between activity-specific energy expenditure and VeDBA (Diving, Transiting,
236 and Surface movement). Finally, we compared estimated total energy expenditure from the best
237 models to DLW measurements to determine the accuracy of different method. All results are
238 means \pm SE.

239 **Results**

240 Three DD tags failed to record any data and 4 stopped recording before the end of the
241 foraging trip. Seven females also came back on land with blood H and O isotopic levels too close
242 to initial background levels to yield accurate metabolic rate measurements and were removed
243 from further analyses. Consequently, sample size for analyses that only required acceleration
244 data or that only required energy expenditure data was $n = 16$ for NFS and $n = 17$ for AFS.
245 However, females missing acceleration data were usually not the ones also missing metabolic
246 rate measurements. Consequently, sample size for analyses in which energy expenditure and
247 acceleration data were combined was $n = 12$ for northern and $n = 13$ for Antarctic fur seals

248 *Diving and foraging behaviours*

249 The female northern fur seals weighed on average of 37.9 ± 1.3 kg (30.8 – 55.6 kg) prior
250 to departure and female Antarctic fur seals weighed 31.0 ± 0.8 kg (25 – 39 kg). Foraging trips
251 lasted 7.96 ± 2.17 d (4.26 - 12.03 d) over 750 ± 50 km (391 - 1200 km) for NFS, and 7.65 ± 3.88
252 d (2.34 - 15.47 d) and 635 ± 77 km (225 - 1295 km) for AFS (both $p > 0.221$). Both species of
253 fur seals spent similar amount of time diving ($\sim 29\%$, $p = 0.328$) and transiting fast at the surface
254 (26 - 30%, $p = 0.063$, Table 1). They also spent $\sim 1/3$ of their time performing slow movements
255 at the surface (28 - 36%), but Antarctic fur seals spent slightly more time doing so than northern
256 fur seals ($p = 0.013$). Conversely, both species spent the smallest proportion of their time resting
257 and sleeping at the surface, ($\sim 8 - 10\%$, $p = 0.401$).

258 *Total energy expenditure versus VeDBA*

259 Energy expenditure while foraging at sea were not significantly different in northern and
260 Antarctic fur seals (155.10 ± 13.01 MJ for NFS and 121.41 ± 17.06 MJ for AFS, $p > 0.09$). The
261 same was true for energy expenditures per day whether for the total DLW time (20.02 ± 1.27
262 MJ/d for NFS and 17.02 ± 1.08 MJ/d for AFS, $p = 0.082$) or for the at-sea time only ($20.93 \pm$
263 1.47 MJ/d for NFS and 17.72 ± 1.15 MJ/d for AFS, $p = 0.097$). Averaging dynamic body
264 acceleration over the entire foraging trip (and for each type of activity, see below and in Table 1)
265 showed that total average VeDBA was overall greater for AFS (0.411 ± 0.02 m/s² or $0.013 \pm$
266 0.001 m/s²/kg) than for NFS (0.312 ± 0.014 m/s² or 0.008 ± 0.0005 m/s²/kg, $p < 0.0004$).
267 Average VeDBA over the entire foraging trip only explained ~ 36% of variability in energy
268 expenditure at sea ($R^2 = 0.36$, Fig. 1 A). Rate of energy expenditure (in MJ/d) is not accurately
269 predicted by acceleration (Fig.1 B, $R^2 = 0.15$). Similar trends were observed for similar analyses
270 when parameters were not mass standardized, but accuracy was overall lower ($R^2 = 0.30$ for EE
271 (MJ) vs VeDBA (m/s²) and $R^2 = 0.08$ for EE (MJ/d vs VeDBA (m/s²)).

272 *Activity-specific energy expenditure versus activity-specific VeDBA*

273 When split by activity, VeDBA was the greatest when the animals were either transiting
274 (0.414 ± 0.013 m/s² for NFS and 0.556 ± 0.026 m/s² for AFS, $p < 0.05$) or active at the surface of
275 the water (0.456 ± 0.22 m/s² for NFS and 0.605 ± 0.017 m/s² for AFS, $p < 0.05$). VeDBA while
276 diving was significantly lower than any surface activity (0.297 ± 0.013 m/s² for NFS and $0.310 \pm$
277 0.018 m/s² for AFS, $p < 10^{-6}$, no difference between species $p > 0.05$). See Table 1 for mass-
278 corrected estimates of activity-specific VeDBA. When animals were resting and sleeping at the
279 surface, VeDBA was the lowest, but was still significantly greater than 0 for both species ($p <$
280 10^{-16}), which suggests there was significant residual dynamic acceleration due to external factors
281 (waves, etc..) when the seals were lying on the water surface (quantification and analyses of
282 these factors can be found in Jeanniard du Dot (2015).

283 Energy spent performing each type of activity (MJ/kg) was significantly related to
284 activity-specific VeDBA when standardized for time spent performing activities (m/s²/kg×d, Fig.
285 2). VeDBA/EE relationships improved greatly when split by type of activity rather than over the
286 full foraging trip (all $R^2 > 0.85$). Both species had similar mechanic-to-energy (VeDBA/EE)
287 efficiencies while diving, but differences in slopes indicate that they differed while transiting or

288 during surface activity. Regression slopes are lower during transiting and surface activity than
289 while diving. Specific equations for diving, transiting and surface activity from Fig. 2 included:

290 Eq. 1 $EE_{\text{Dive}} \text{ (MJ/kg)} \sim (0.10 \pm 0.10) + (91.99 \pm 4.42) \times \text{VeDBA}_{\text{Dive}} \text{ (m/s}^2\text{/kg*d)} + (0.14 \pm$
291 $0.08 \text{ for NFS only}); R^2 = 0.94, \text{ slope } p < 2.10^{-16}$

292 Eq. 2 $EE_{\text{Transit}} \text{ (MJ/kg)} \sim (0.14 \pm 0.05) + (27.62 \pm 1.11) \times \text{VeDBA}_{\text{Transit}} \text{ (m/s}^2\text{/kg*d)}$
293 $+ [(0.06 \pm 0.08) + (10.19 \pm 2.54) \times \text{VeDBA}_{\text{Transit}} \text{ for NFS only}]; R^2 = 0.96,$
294 $\text{slope } p < 2.10^{-16}$

295 Eq. 3 $EE_{\text{Surf}} \text{ (MJ/kg)} \sim (0.06 \pm 0.07) + (23.40 \pm 1.48) \times \text{VeDBA}_{\text{Surf}} \text{ (m/s}^2\text{/kg*d)} +$
296 $[(0.22 \pm 0.06) \times \text{VeDBA}_{\text{Surf}} \text{ for NFS only}]; R^2 = 0.90, \text{ slope } p < 2.10^{-15}$

297 Similar analyses with parameters that were not mass-standardized were once again not as
298 accurate as the mass standardized ones above, but all R^2 were still above 0.89.

299 *Predicting total energy expenditure at sea from activity-specific DBA*

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

303 Eq. 4 $\text{Total } EE_{\text{Pred.}} \sim EE_{\text{Dive}} + EE_{\text{Transit}} + EE_{\text{Surf}}$

304 Total energy expenditure estimated from Eq. 4 correlated well with measured total energy
305 expenditure from the DLW method ($R^2 = 0.70$, Fig. 3A). There was no systematic differences
306 between observed and simulated values (slope of the linear regression not significantly different
307 from 1 (1.00 ± 0.14 , $p < 4.10^{-7}$) and intercept not significantly different from 0 ($1.10^{-15} \pm 0.56$, p
308 $= 1$) so our model yielded appropriate estimates of total energy expenditure.

309 **Discussion**

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

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

321 *Dynamic Body Acceleration as a predictor of energy expenditure during a full foraging trip*

322 Our results show that average VeDBA over a full trip is not an accurate predictor of
323 energy expenditure and could only explain 36 % of its variation (Fig. 1A). This R^2 is lower than
324 values reported for other vertebrates measured in captivity/semi-captivity (0.47 for diving Steller
325 sea lions, Fahlman *et al.* 2008; 0.84 in birds, Halsey *et al.* 2009a; 0.60 for swimming sharks,
326 Gleiss *et al.* 2010; 0.56 for turtles, Halsey *et al.* 2011). The poor ability of VeDBA to predict
327 energy expenditure over a full trip is likely related to the assumptions behind VeDBA as a proxy
328 for energy expenditure and/or in the sources of unmeasured error associated with free-ranging
329 environmental conditions (Gleiss, Wilson & Shepard 2011; Halsey, Shepard & Wilson 2011).

330 First, most studies have validated VeDBA in captive or semi-captive settings, i.e. in
331 controlled conditions (Wilson *et al.* 2006; Gleiss *et al.* 2010; Halsey *et al.* 2011; Fahlman *et al.*
332 2013). However, free-ranging marine animals live in a dense medium under fluid environmental
333 conditions and seals spend a significant portion of their time at the water surface, where wind-
334 related motions, mainly through wave action can interfere with energy expenditure and the
335 dynamic body acceleration signal. This residual 'environmental' acceleration largely disappears
336 when the animals dive and is consistent between seals over their foraging trips. It can thus be
337 corrected, but it still impacts the slope of the VeDBA/EE relationships (Jeanniard du Dot 2015).
338 Another difference between other validation studies and ours is the variation in the duration of
339 measurements taken (i.e., hours vs. days or weeks). In our case, the northern and Antarctic fur
340 seals undertook foraging trips that averaged 7 - 8 days (range 2.5 - 15 days). A fur seals that
341 makes a long foraging trip is likely to allocate energy differently compared to an animal that
342 makes a short trip, yet averaging VeDBA over time does not account for such differences. We
343 suspect this is why none of our analyses that used metabolic rate as our reference measurement
344 (in MJ/d, Fig. 1 B) yielded significant relationships with VeDBA, unlike in other studies.

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

360 In addition to the uncertainties associated with VeDBA discussed above, there are also
361 inherent uncertainties with using the doubly-labelled water method (DLW) as our reference
362 measure of energy expenditure that might affect accuracy of our EE/VeDBA relationship. Some
363 studies of specialist marine carnivores have suggested that the DLW method has high accuracy,
364 but low precision (Speakman 1993). For example, the DLW method applied to grey seals
365 (*Halichoerus grypus*) subjected to simulated foraging conditions over 5-day periods yielded
366 estimates of energy expenditure for groups averages that were similar to estimates derived from
367 respirometry (group error was 0.5%, Sparling *et al.* 2008), but individual error was $\sim \pm 40\%$.
368 Similarly, a study of captive northern fur seals showed that the average error of the DLW method
369 compared to respirometry measurements could be as low as $\sim 0.8\%$ but as high as $\sim 27\%$
370 depending on the calculation method used and the time of year (lowest in the fall and highest in
371 the summer, Dalton, Rosen & Trites 2014). Consequently, the error associated with our reference
372 measurement of energy expenditure is likely significant since we compared DLW to VeDBA
373 measurements at the individual level (one DLW and one VeDBA point per animal). We
374 recognize that using DLW measurements as a reference measurement of energy expenditure

375 comes with associated caveats, but was the only option available to us to study energy
376 expenditure at sea for free-ranging fur seals.

377 Either way, there seems to be no escaping the fact that VeDBA metrics are not an
378 appropriate means to predict the total energy expended regardless of method used to establish the
379 reference energy expenditure, especially when measured over long periods of time in the wild
380 when animals engage in different behaviors that have markedly different energetic costs (Green
381 *et al.* 2009; Halsey, Shepard & Wilson 2011; Dalton, Rosen & Trites 2014). A study of free-
382 ranging thick-billed murre (*Uria lomvia*), for example, found that activity-specific VeDBAs
383 were better predictors of energy expenditure during a foraging trip than overall VeDBA,
384 especially if one activity type had a greater energetic cost than others (in this case flying, Elliott
385 *et al.* 2013). Animals are known to incur different energetic costs to undertake different
386 activities, and different relationships are known to exist between VeDBA and EE depending on
387 gaits in humans (Halsey *et al.* 2008), intensities of swimming in sharks (Gleiss, Gruber & Wilson
388 2009) and types of muscles involved in the movement of birds (Gomez-Laich *et al.* 2008). All
389 told, this suggests that the poor ability of total VeDBA to predict the energetic cost of foraging
390 trips undertaken by our fur seals might be due to differences in time-activity budgets (i.e., how
391 the animals partitioned their time at sea between diving, transiting, resting and surface activities).

392 *Time-activity budgets and activity-specific energy expenditures*

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

402 Changes in DBA affect mechanical power and thus energy expenditure more drastically
403 while diving than while transiting or during surface activities (Fig. 2). This means that small
404 changes in measures of DBA can lead to larger changes in estimates of diving energy

405 expenditure than of energy spent in surface behaviours. Why diving has inherently the lowest
406 VeDBA but the highest costs compared to other activities is likely due to the fact that animals
407 have to compromise between high speeds to maximize time foraging at depth and drag that
408 increases with swimming velocity (Costa & Williams 1999). In comparison, transiting also
409 involve high speed swimming but it is usually done either at depths where drag is the lowest (i.e.,
410 at 3 body diameter depth, Williams 1989; Hindle, Rosen & Trites 2010), or by porpoising which
411 increases locomotion efficiency (Boyd 2002). Slow surface movements also occur at the surface
412 where drag is high, but movements are at lower velocity when drag is decreased (Costa &
413 Williams 1999).

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

424 As mentioned earlier, DLW is known to lack precision at the individual level but to
425 provide estimates of energy expenditure with a reasonable accuracy at the group or population
426 level (Speakman 1993). Unlike full foraging trip models in which individual DLW
427 measurements were compared to overall acceleration, activity-specific models compared
428 activity-specific acceleration to the energy that each animal spent per activity (in MJ) calculated
429 using parameter estimates of Eq. 2 from Jeanniard du Dot *et al.* (In review). These parameter
430 estimates provide average metabolic rates per activity (in MJ/d) over all study animals, i.e. at the
431 group level. Consequently, using 'group' metabolic rates in the activity-specific models might
432 improve accuracy of predictions for total energy expenditure by reducing the individual errors
433 associated with DLW measurements. This means that ~20 - 35% of the uncertainty in the global
434 model could be attributed to errors in the DLW measurements and individual variability in time-

435 activity budgets and foraging strategies (even if it was impossible to tease apart the respective
436 effects of these two parameters).

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

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

457 In a finer scale study, Skinner *et al.* (2014) also found that VeDBA multiplied by distance
458 traveled, mass of the animal, and vertical distance swam were together the best metrics to assess
459 energy expenditure of northern fur seals at sea. We applied the best model from Skinner *et al.*
460 (2014) to our data and only obtained an $R^2 = 0.50$. However, there are parallels in our two
461 respective models in that both take into account effort and time spent diving versus other
462 activities (see Table 2.4 in Jeanniard du Dot 2015). Both models point out that knowing how
463 much time an animal spends foraging, diving, transiting and being surface active is as important
464 as knowing the intensity with which the seals perform these activities.

465 *Conclusions*

466 All in all, our results show that the time a seal decides to allocate to activities that have
467 different metabolic rates is important for obtaining accurate estimates of energetic costs of
468 foraging in fur seals. Estimates of total energy expended by fur seals should thus be done using
469 the activity-specific DBA paired with time-activity budget (i.e., Eq. 4). It also emphasizes the
470 potential for acceleration to determine behavioural activity budgets and energy expenditures
471 under wild conditions and over a wide range of activities at a much finer scale than more
472 traditional location and depth loggers, and at temporal and spatial scales that are relevant to
473 ecological studies. In any case, being able to accurately calculate foraging costs helps to better
474 understand the energetic requirements of free-ranging seals and other marine mammals, and
475 whether they can be met in the wild. Knowing foraging costs also contributes to assessing the
476 ecological impacts that marine mammals have on trophic webs, and how changes in time-activity
477 budgets due to environmental changes affect their fitness. Such knowledge is particularly
478 important for the conservation and management of species that are easily impacted by ecosystem
479 shifts and environmental changes, especially for fur seals that are already performing close to
480 their metabolic ceilings, and may have limited scope to adapt to coming climate changes.

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489 approval from the French Polar Institute (IPEV).

490 **Data accessibility**

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

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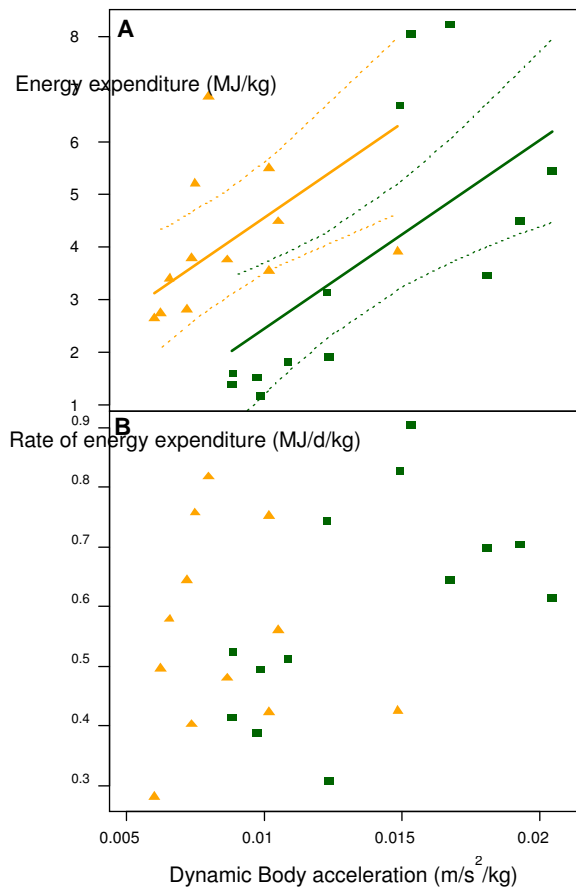
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682 **Figures**

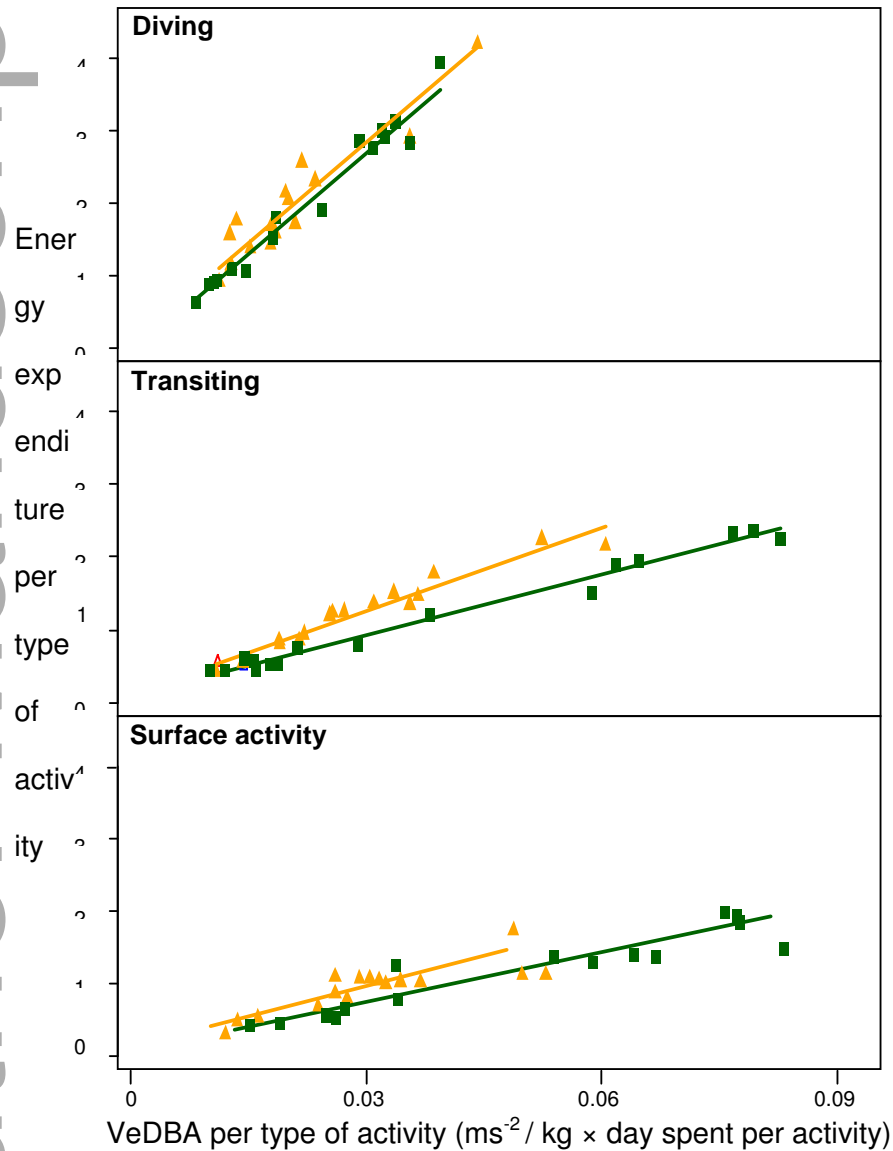
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684 Figure 1: Relationships for northern fur seals (yellow triangles) and Antarctic fur seals (green
685 squares) between energy expenditure in MJ/kg (A) or rate of energy expenditure in MJ/d/kg(B)
686 and the average dynamic body acceleration over the entire foraging trip in m/s²/kg. Each data

687 point represents a single animal and was mass corrected. Panel A: $R^2 = 0.36$, AIC = 102.1, slope
688 $p = 0.002$, species $p = 0.02$. Panel B: there were no significant species-specific relationships
689 between VeDBA and the rate of energy expenditure.

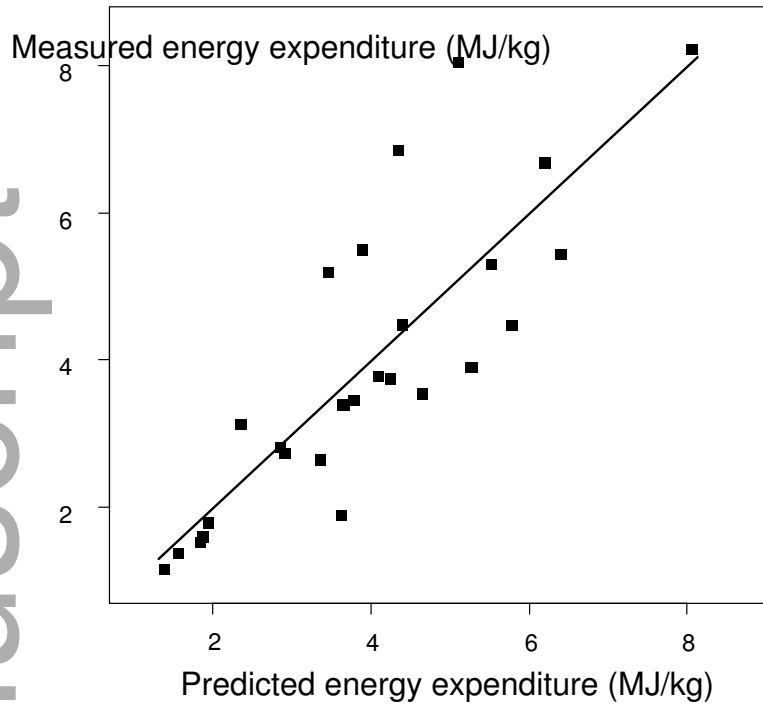
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691 Figure 2: Relationships between activity-specific VeDBA standardized for individual time-
692 activity budgets and body mass and activity-specific energy expenditure in MJ/kg for lactating
693 northern fur seals (triangle symbols, n=16) and Antarctic fur seals (square symbols n=16). Plain
694 lines show the results of linear models that included species as an independent variable.

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697 Figure 3: Comparison between measured energy spent at sea by lactating northern and Antarctic
 698 fur seals using the DLW method, and the predicted energy expenditure estimated using Eq. 5.
 699 The regression line has an intercept of $1.4 \times 10^{-15} \pm 0.56$, not statistically different from 0, and a
 700 slope of 1.00 ± 0.13 , not statistically different from 1, $R^2 = 0.70$.

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703 Tables

704 Table 1: Proportion of total time at sea and average VeDBA spent in 4 types of activity for 16
 705 lactating northern fur seal and 17 lactating Antarctic fur seal during a single foraging trip.
 706 Activities included active foraging (diving + post dive surfacing), resting at the surface,
 707 transiting at a speed greater than 1m/s, and slow surface movements (< 1m/s) / grooming. Gap
 708 refers to the proportion of time when data were missing and could not be allocated to either of
 709 the 4 activity types. Values are means \pm SE and asterisks show the values significantly different
 710 between species.

Activity type	Proportion of at-sea time in each activity (%)	Average VeDBA during each type of activity ($m/s^2/kg$)
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	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

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