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3   **Relationships grow with time: a note of caution about energy expenditure-proxy correlations,**
4   **focussing on accelerometry as an example**

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14   **Summary**

15   Scientists studying the energy expenditure of air-breathing divers are interested in developing a
16   more tractable technique to support their endeavour. Accelerometers instrumented to animals can
17   return a tangible measure of those animals' activity levels, which in some situations correlates with
18   their metabolic rate. However, I argue that reported evidence for this correlation in semi-aquatic
19   animals while diving is not always as strong as it seems. This is because some analyses have derived
20   a measure of activity level by calculating the *sum* of accelerometry-based values and compared
21   those data points to measures of *summed* (total) energy expenditure. These summations mean that
22   time (duration) has been introduced into both sides of the regression equation. This is likely to
23   generate a correlation between body acceleration and energy expenditure even if the two variables
24   are not mechanistically linked because time will correlate with itself. Thus a strong relationship
25   between a summed measure of energy expenditure and a summed proxy of energy expenditure
26   indicates only that as time passes an animal burns calories. Issues concerning summation of
27   variables in principle extend to other potential proxies of energy expenditure, such as heart rate. I
28   demonstrate the artefactual effect of regressing summed values with analyses of modelled data
29   using ecologically valid parameters. Unless a summed proxy predicts total energy expenditure
30   substantially better than does time alone there is little evidence upon which to base a claim that
31   body acceleration is suitably predictive of metabolic rate. Clarity about the predictive power of body
32   acceleration to estimate metabolic rate should be sought by simply presenting a graph of the
33   relationship between these raw values.

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36 **Main text**

37 Animals that dive underwater are fascinating, but rather hard to study. Because diving animals must
38 breath-hold, yet are able to do so for extended periods, much research has focussed on their rates
39 of energy expenditure while underwater (Butler & Jones 1997), which have considerable influence
40 on their foraging durations (Halsey, Butler & Blackburn 2006). In the laboratory, or using trained
41 animals in the field, diving animals can be taught to surface into a respirometer hood and thus their
42 rate of oxygen consumption measured to quantify their metabolic rate (Halsey, Woakes & Butler
43 2003). But this technique cannot be applied to fully wild individuals. In such cases our option is to
44 deploy data logging devices on wild individuals that measure a proxy of energy expenditure.
45 Beginning in the 1970s, Professor Pat Butler and his lab at the University of Birmingham progressed
46 the application of the 'heart rate technique' (initially developed by Eliassen 1960) to study the
47 energy expenditure of diving animals (e.g. Butler & Woakes 1975). Heart rate loggers are surgically
48 implanted and later retrieved through a capture-release-recapture protocol. Heart rate tends to
49 correlate with metabolic rate (Boothby 1915); the harder an animal is working the faster its heart
50 beats to support up-regulation of the cardio-respiratory system.

51 The technique has, and continues to be, key in elucidating the energy budgeting of diving animals,
52 typically at the scale of at least the dive cycle (Froget *et al.* 2004) (but see also (Green *et al.* 2007)).
53 However, as is well documented, the heart rate technique is logistically demanding (Green 2011).
54 Two aspects that have been the chagrin of many a practitioner are the general need to implant the
55 heart rate loggers, and even then the uncertainty that a strong electrocardiogram (ECG) will be
56 recorded. So for a long time there has been interest in an alternative proxy for metabolic rate, which
57 is easy to measure in wild animals. In 2005, Professor Rory Wilson, myself and others devised a plan
58 to demonstrate that the whole-body activity of an animal can be recorded with a data logger and
59 will relate to its metabolic rate, based on the simple premise that more energy is expended during
60 periods of high activity (Gleiss, Wilson & Shepard 2011). Acceleration data loggers (accelerometers)
61 had already been applied in animal research to remotely quantify behaviour (Yoda *et al.* 2001;
62 Watanuki *et al.* 2003), demonstrating that these devices recognise changes in activity. Rory Wilson
63 developed the metric now termed dynamic body acceleration (DBA), which can easily be derived
64 from acceleration data and represents a broad measure of the animal's level of movement at a given
65 moment in time – its rate of activity. We needed to demonstrate that DBA correlated with metabolic
66 rate, but neither Rory Wilson nor I had access to laboratory animals. Once again the University of
67 Birmingham was involved; an ongoing project there studying captive birds provided us with the
68 opportunity. Cormorants walking on a treadmill were an unlikely model, but they allowed us to
69 demonstrate that as the birds walked faster, not only did their metabolic rate increase but so did the
70 acceleration of their trunk to which an accelerometer was attached (Wilson *et al.* 2006).

71 *The accelerometry technique applied to diving animals*

72 In the following few years, a growing number of lab-based studies were painting the encouraging
73 picture that DBA correlated well with metabolic rate during activity in a great diversity of taxa from
74 birds (Wilson *et al.* 2006; Green *et al.* 2009; Halsey *et al.* 2009b) and mammals (Halsey *et al.* 2008;
75 Halsey *et al.* 2009b) to amphibians (Halsey & White 2010), fish (Clark *et al.* 2010; Gleiss *et al.* 2010)
76 and cuttlefish (Payne *et al.* 2011).

77 However none of these studies investigated animals while they were diving. A relationship between
78 energy expenditure and DBA in diving animals might be predicted because, similarly to the treadmill
79 scenario, dives involving greater activity are associated with higher rates of energy expenditure
80 (Halsey, Woakes & Butler 2003). In contrast to typical situations on land, however, diving involves

81 the complicating issues of intermittent breathing, a lack of a physiological steady state (Fedak, Pullen
82 & Kanwisher 1988), and possibly changes in regional body temperatures affecting metabolism
83 (Gremillet, Tuschy & Kierspel 1998; Enstipp, Grémillet & Jones 2006; Lovvorn 2007). Further possible
84 complications associated with measuring energy expenditure during breath-hold diving are
85 discussed in Halsey et al. (2011a). Given the value of data loggers to the study of semi-aquatic
86 animals it was important to find out whether accelerometers could be used to estimate their energy
87 expenditure during diving.

88 Cormorants again provided the model for this test of the accelerometry technique, but this time we
89 ran the experiments at the University of British Columbia, taking advantage of their impressive 10 m-
90 deep dive tank (Figure 1a). This super-sized laboratory environment allowed the birds to undertake
91 repeated dives to the sort of depths they reached in the wild. They were required to surface each
92 time into a respirometry hood (Figure 1b). Our data showed a strong correlation between total
93 oxygen consumed by a bird each dive cycle (a dive and the subsequent surfacing period of recovery)
94 and a summation of DBA over the same period (Halsey *et al.* 2011b [their Figure 1]). This concurred
95 with data published some years before by Williams et al. (2004) on Weddell seals *Leptonychotes*
96 *weddelli*, showing a strong relationship between total oxygen consumed and the total number of
97 strokes performed during a dive; stroke count had been estimated from a one-axis accelerometer
98 (Williams *et al.* 2004 [their Figure 5b]). Some recently published studies present results that also
99 concur with these findings by demonstrating that similar relationships hold for semi-aquatic animals
100 exhibiting a range of natural behaviours which include extensive diving. Summed DBA in
101 combination with initial body mass and distance travelled is a strong predictor of mass change
102 (which is closely related to total energy expenditure; Croxall 1982) in northern fur seals *Callorhinus*
103 *ursinus* (Skinner *et al.* 2014). Jeanniard-du-Dot *et al.* (2016 [their Figure 2]) present strong
104 relationships between total energy expended and summed DBA across foraging trips in both
105 northern and Antarctic fur seals (*Callorhinus ursinus* and *Arctocephalus gazella*). The same authors
106 followed up with a second publication on the same species indicating strong relationships between
107 total energy expended and cumulative flipper beats (interpreted from accelerometry data)
108 specifically during periods of diving (Jeanniard-du-Dot *et al.* 2016 [their Figure 1]), and a similar
109 relationship was reported in northern elephant seals *Mirounga angustirostris* by Maresh et al.
110 (Maresh *et al.* 2014; Maresh *et al.* 2015). Stothart et al. (2016 [their Figure 3a]) report as part of
111 their findings a very strong relationship between summed DBA and mass-specific total energy
112 expenditure during daily activities in a diving cormorant *Phalacrocorax pelagicus*.

113 Yet none of these findings indicate that mean DBA correlates with metabolic rate. Why?

114 *The time trap*

115 In each of these aforementioned analyses, both energy expenditure and DBA (or flipper strokes
116 interpreted from accelerometry) were calculated as *summations* over the data collection period (e.g.
117 a dive cycle or foraging bout), with one data point per animal. Thus when testing for a correlation,
118 *total* energy expended was regressed against *total* DBA. Of course, the longer an animal is wearing
119 an accelerometer logger the greater the summed acceleration stored on the logger and at the same
120 time the greater the animal's total energy expenditure; both variables are increasing inexorably over
121 time (Figure 2a). If the duration of the measurement period varies between animals, and thus
122 between data points, in the regression, as was the case in each of the aforementioned studies, then
123 time will correlate with itself. In other words, a correlation can exist between summed acceleration
124 and total energy expenditure but be driven entirely by the fact that summation of the two variables
125 has brought time into both sides of the equation (Figure 2b). In turn, this finding alone provides no
126 evidence for a relationship between DBA and metabolic rate; interpreting that it does can be

127 considered as falling into the 'time trap'. This trap is not set for accelerometry alone, but is in
128 principle awaiting any proxy measure of metabolic rate.

129 In our diving cormorant paper, we went on to show that there was a complete lack of relationship
130 between *rate* of oxygen consumption and *mean* DBA (at the scales of both dives and diving bouts;
131 Halsey *et al.* 2011b [their Figures 3 and 4]). We also made the argument that the correlation for
132 Weddell seals reported by Williams et al. (2004) only arose because their analysis had fallen into the
133 time trap. The R^2 reported for the relationship between total oxygen consumed and the number of
134 strokes performed during a dive (0.87) was very similar to that obtained when total oxygen
135 consumption was instead regressed against time (dive duration; $R^2 = 0.85$). (The addition of a
136 random variable to a regression is quite likely to improve the R^2 by at least 0.02). This suggests that
137 the number of strokes taken by the seals correlated with their total oxygen consumption only
138 because both variables were correlated with dive duration. Furthermore, in Halsey et al. (2011b) we
139 reported on a reanalysis of data presented for a relationship between rate of oxygen consumption
140 and mean DBA in Steller sea lions *Eumetopias jubatus* (Fahlman *et al.* 2008); the one other analysis
141 which by that time had attempted to calibrate DBA in a semi-aquatic species during diving
142 behaviour. Our reanalysis returned an R^2 value of just 0.14 (Halsey *et al.* 2011b).

143 Despite consideration of the time trap being prominent in the discussion of our diving cormorant
144 study, it appears that the warnings we offered have often been ignored (though see Stothart *et al.*
145 2016). Indeed, our cormorant study has been repeatedly cited as an example of the validity of the
146 accelerometry technique for diving animals (Elliott *et al.* 2012; Skinner *et al.* 2014; Jeanniard-du-Dot
147 *et al.* 2016). And in recent years I have refereed a number of submitted manuscripts from a host of
148 research groups where analyses have centred around summed values of energy expenditure and
149 DBA to test for evidence that DBA relates to metabolic rate; sometimes other referees for these
150 manuscripts have suggested summing values as an improvement to the analysis.

151 There is an ever growing interest in the application of the accelerometry technique to a broadening
152 array of species (Mosser *et al.* 2014; Williams *et al.* 2014), and a keenness to demonstrate this
153 relatively tractable method for measuring energy expenditure in wild animals. It is therefore of
154 paramount importance that researchers understand how easy it is to fall into the time trap, and how
155 readily this trap springs even if the underlying measures of metabolic rate and activity levels are
156 wholly unrelated to each other.

157 To impress this point, in the current article I present this concept graphically, using simulated
158 datasets, generated in R (R Development Core Team 2011), comprising multiple independent paired
159 measurements of ecologically valid metabolic rate and DBA recorded for a study species. This was
160 achieved by randomly generating the model's input values (metabolic rate, DBA and logger
161 recording duration), assuming a flat underlying distribution, within the ranges for those values
162 reported in one of the aforementioned papers (Jeanniard-du-Dot *et al.* 2016) for northern fur seals.
163 In my view this paper, for the reason argued in this article, concludes there is a strong relationship
164 between energy expenditure and DBA without presenting sufficient evidence. Specifically, the model
165 presented in the current study has the same number of data points (animals) to that of Jeanniard-
166 du-Dot *et al.* (2016), and a similar mean and spread of recording durations associated with those
167 data points. The range of metabolic rates and the range of mean DBA values were also very similar
168 to those presented in that empirical study. Within this framework, the random generation of
169 metabolic rate and mean DBA values simulated the sampling of two variables that are unrelated.
170 Modelled metabolic rate was then summed to calculate total energy expenditure, i.e. it was
171 calculated as the product of metabolic rate and recording duration (time). Summed DBA was
172 calculated as the product of mean DBA and time. Finally, the R^2 values were calculated for the linear

173 regression of metabolic rate against mean DBA, and total energy expenditure against summed DBA.
174 10 000 iterations of the model were run.

175 As would be expected for two randomly generated variables, the relationship between metabolic
176 rate and mean DBA was typically negligible (Figure 3a and c, and Figure 4a). Mean $R^2 \pm 1$ standard
177 deviation was 0.10 ± 0.12. The relationship between total energy expenditure and summed DBA was
178 most commonly of medium strength (Figure 3b). However, it varied around this mean value
179 encompassing almost the full range of possible R^2 values (0 to 1; Figure 4b). Mean $R^2 \pm 1$ standard
180 deviation for this relationship was 0.50 ± 0.20. The mean R^2 value is therefore improved by the
181 inclusion of time to both sides of the regression equation by on average 0.40 (Figure 3a v. Figure 3b).
182 The frequency distribution of R^2 values for the relationship between total energy expenditure and
183 summed DBA was Gaussian, indicating that in around half of the simulations R^2 was even higher than
184 0.5. Thus the chances of generating a relationship returning an R^2 considerably higher than 0.5
185 despite metabolic rate and mean DBA being entirely unrelated is substantial (Figure 3d).

186 *Concluding thoughts*

187 The allure of diving animals is unabated; rightly so researchers continue to be captivated by their
188 breath-holding feats and there is much still to learn (Elsner 2015). Despite the development of the
189 heart rate technique (Green *et al.* 2007) and other methods such as the doubly-labelled water
190 technique (Shaffer 2011), obtaining accurate estimates of energy expenditure in submerged divers is
191 still laden with difficulties (Butler *et al.* 2004; Halsey 2011). It is therefore understandable that
192 researchers want the accelerometry technique to work with such creatures. And there is evidence
193 that, at least for sea turtles, it does. Both Enstipp et al. (2011) and Halsey et al. (2011a) reported
194 strong lab-derived relationships between metabolic rate and mean DBA during diving bouts in green
195 turtles *Chelonia mydas*.

196 However, given that the models presented in the current article demonstrate how the time trap can
197 produce good relationships between energy expenditure and DBA when the two variables are not
198 mechanistically linked, the conclusion from the literature thus far must be that there is a lack of
199 compelling evidence for a metabolic rate-mean DBA relationship in any other taxon while diving.
200 And this is supported by a string of papers on pinnipeds broadly concluding that there is little
201 evidence the accelerometry technique works on these species when they are at sea (Dalton, Rosen
202 & Trites 2014; Skinner *et al.* 2014; Volpov *et al.* 2015; Volpov *et al.* In Press); see also Rosen *et al.*
203 (2016). Finally, while there is some evidence that in seabirds the relationship can arise across a
204 broad array of behaviours that include diving, it is unclear whether the relationship holds during
205 diving periods alone (Elliott *et al.* 2012; Stothart *et al.* 2016).

206 Halsey et al. (2011a) in particular discuss possible reasons why there is this contrasting success for
207 the accelerometry technique between turtles and other species (see also Elliott *et al.* 2012; Volpov
208 *et al.* In Press). For many diving animals their movements may be damped while submerged
209 resulting in activity while at the surface having an unrepresentatively large effect on DBA,
210 exacerbated by wave action; however, most of the green turtle's body is submerged when it is at the
211 water surface (Halsey *et al.* 2011a). Heat lost during dives can also uncouple energy expenditure
212 from body movement (Gremillet, Tuschy & Kierspel 1998; Enstipp, Grémillet & Jones 2006), but the
213 metabolic rate of green turtles is not thermally dependent at the water temperatures they
214 experience in the wild (Southwood *et al.* 2006). In some scenarios and species, digestion, gliding
215 behaviour and buoyancy may also disrupt the potential relationship between DBA and metabolic
216 rate (Volpov *et al.* In Press).

217 In time it might be shown that, at least under certain conditions, the metabolic rate-mean DBA
218 relationship is also present in species where thus far the evidence for this correlation is poor.
219 Accounting for metabolic suppression during dives (Stothart *et al.* 2016) or the confounding
220 influence of wave action on the body during surface periods (Elliott *et al.* 2012), may offer some
221 routes to uncovering relationships currently hidden. Otherwise, perhaps higher computational
222 analyses of acceleration data, for example including gyroscope or magnetometry data to
223 discriminate linear from rotational motions (López *et al.* 2016; Ware *et al.* 2016) will characterise
224 diving behaviour sufficiently well such that it can be effectively related to metabolic rate, so long as
225 a sufficient portion of metabolic rate is explained by body movements (Halsey, Shepard & Wilson
226 2011; Elliott 2016). Other possibilities include the addition of cameras to clarify how acceleration
227 relates to behaviour details (Cade *et al.*), or combining heart rate and accelerometry measures
228 (Bishop *et al.* 2015), or coupling the accelerometry analysis with biomechanical modelling (Elliott
229 2016).

230 An argument might be made that summing DBA values, while inappropriate for assessing whether
231 higher activity rates are related to a higher metabolic rate, might nevertheless be an effective way to
232 estimate the energy an animal has expended over a given period of time such as a dive or diving
233 bout. After all, summed DBA incorporates both duration and degree of activity, both of which might
234 be good predictors of total energy expenditure. This supposition can only be confirmed, however, by
235 comparing the strength of the relationship with that of the correlation between total energy
236 expenditure and time (alone). In the aforementioned diving Weddell seal example (Williams *et al.*
237 2004), as discussed earlier this comparison did not provide evidence for the predictive power of
238 accelerometry. Indeed, considering flipper beats as the energy expenditure proxy provides a clear
239 image of the mistake made in interpreting cumulative values as evidence for a relationship between
240 rates. The seal's flippers are somewhat analogous to a ticking clock; tick-tock, tick-tock – the beats of
241 the flippers count the accumulation of passing time. And, of course, the model outputs in the
242 present article support this argument, illustrating how a relationship between the summations can
243 exist without any underlying relationship between the rates. The simplest way to separate out the
244 complicating and confounding effects of time when assessing the efficacy of the acceleration
245 technique as a predictor of energy expenditure is to leave time out of the equation.

246 In the present article I do not argue that the accelerometry technique is a poor method for
247 estimating rates of energy expenditure in wild animals; as with all methods, it has its limitations
248 (Halsey, Shepard & Wilson 2011) yet in many scenarios its effectiveness has been demonstrated
249 (Wilson *et al.* 2013; Brodie *et al.* 2016). I also do not argue that accelerometry for estimating rates of
250 energy expenditure is inappropriate for diving animals in general; it has been shown to calibrate in
251 turtles (Enstipp *et al.* 2011; Halsey *et al.* 2011a) and there is also an argument that, at least within
252 individuals, changes in mean DBA may provide qualitative insight into changes in metabolic rate
253 (Halsey *et al.* 2009a; Green 2011; Halsey, Shepard & Wilson 2011). Nor do I even argue that
254 particular species or situations are definitely unsuitable for the technique. Rather, I have suggested
255 that certain studies claiming strong evidence that the technique works for particular species have
256 overstepped the mark, because the time trap has limited the insight of their correlative analyses.
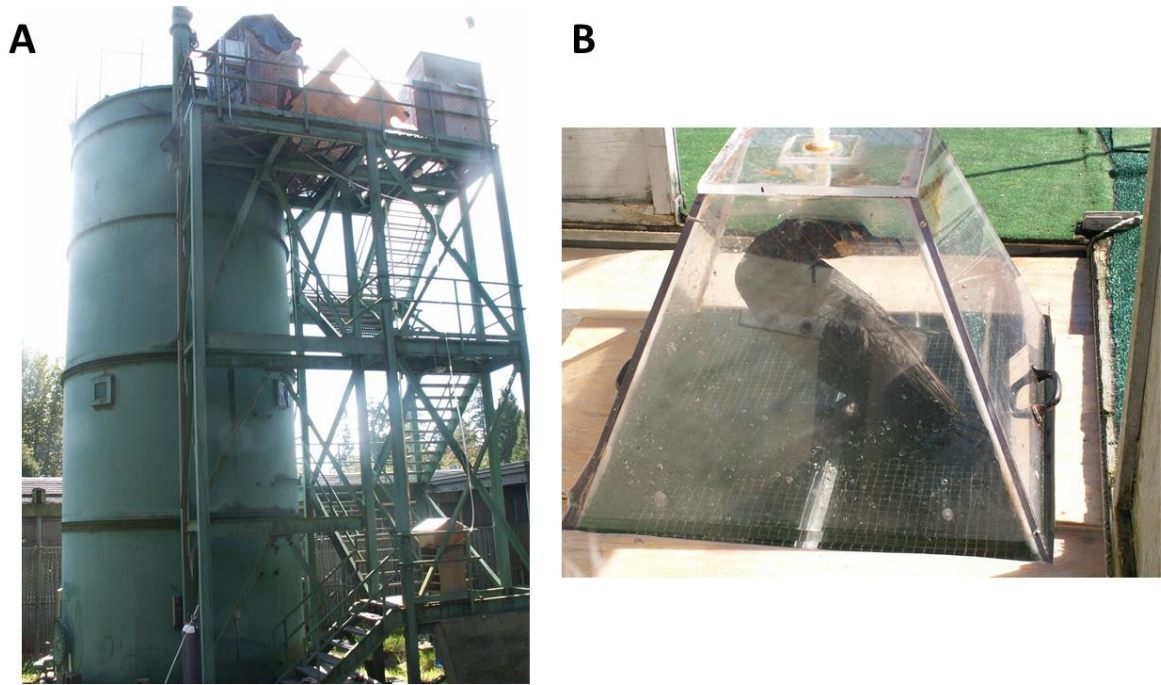
257 When we have gathered data that we believe indicate a relationship between metabolic rate and
258 mean DBA or the mean of any other proxy, for the sake of full disclosure and clarity we should
259 present this key finding as a straightforward plot of the raw values.

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261 Acknowledgements

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Figure 1. (a) The 10-m dive tank at the University of British Columbia. (My colleague Craig White can just be made out standing at the top, in front of the viewing hut). (b) The double-crested cormorants had to resurface after each dive into a respirometry hood, in order that their rates of respiratory gas exchange could be measured. In this photograph, the cormorant has been placed within the hood prior to the start of the experiment. Upon commencement of the experiment, the netting that the bird is standing on falls away to allow the bird access to the water below.

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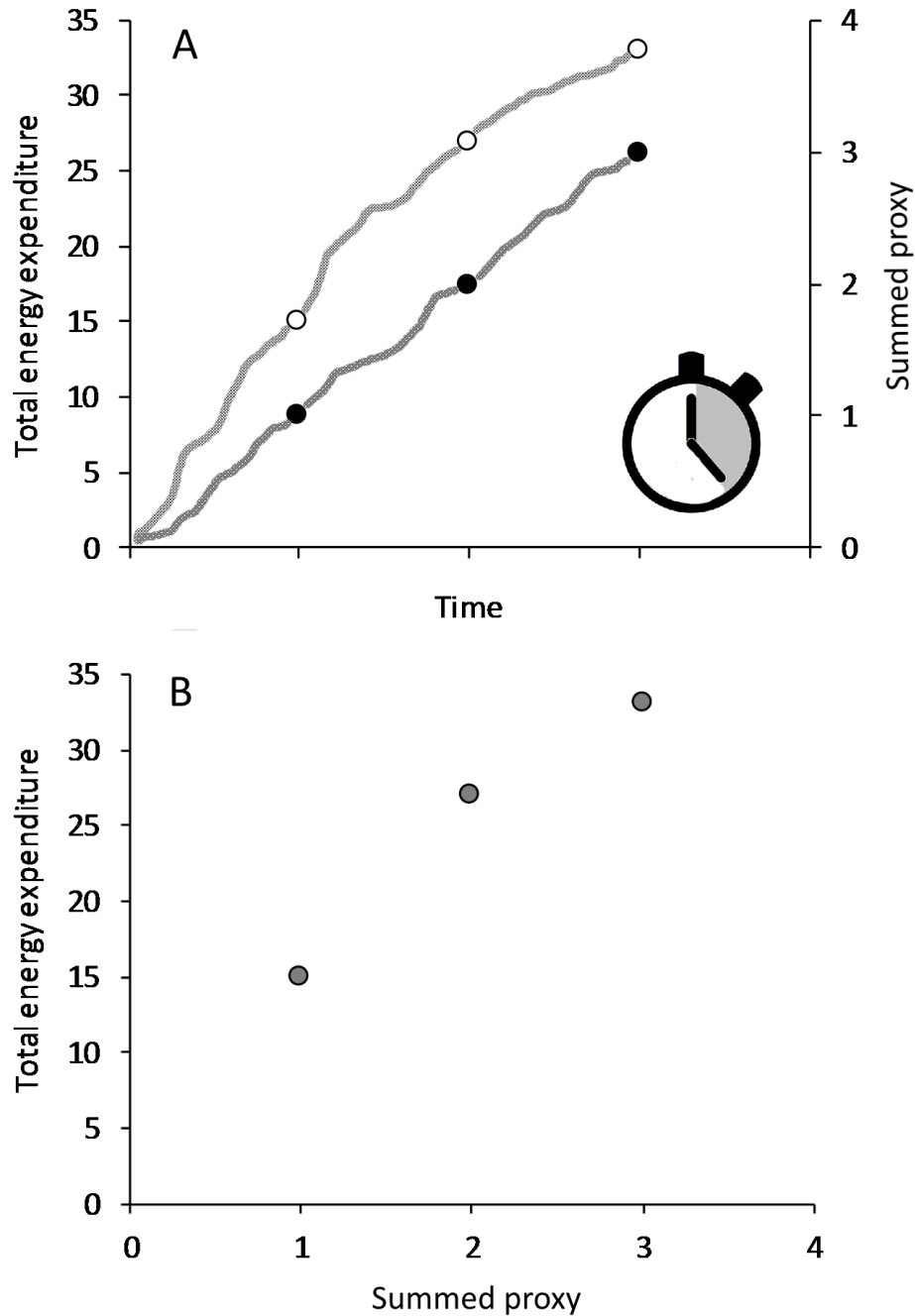
Figure 2. As the time that an experiment has been underway increases, cumulative measures recorded during that experiment inevitably increase in size. (a) The total energy expenditure of an animal in the field will inexorably increase as time passes (upper line), as will summed measures of the proxy recorded on the data logger instrumented to the animal (lower line). I.e. both these variables innately correlate with time. For the same animal or different animals, it is therefore very likely that correlating coupled measures of total energy expenditure (open circles) against a totalled value of the measured proxy (closed circles) taken from distinctly different time points will (b) result in a strong relationship, and this can be driven simply by the relationship between both variables and time.
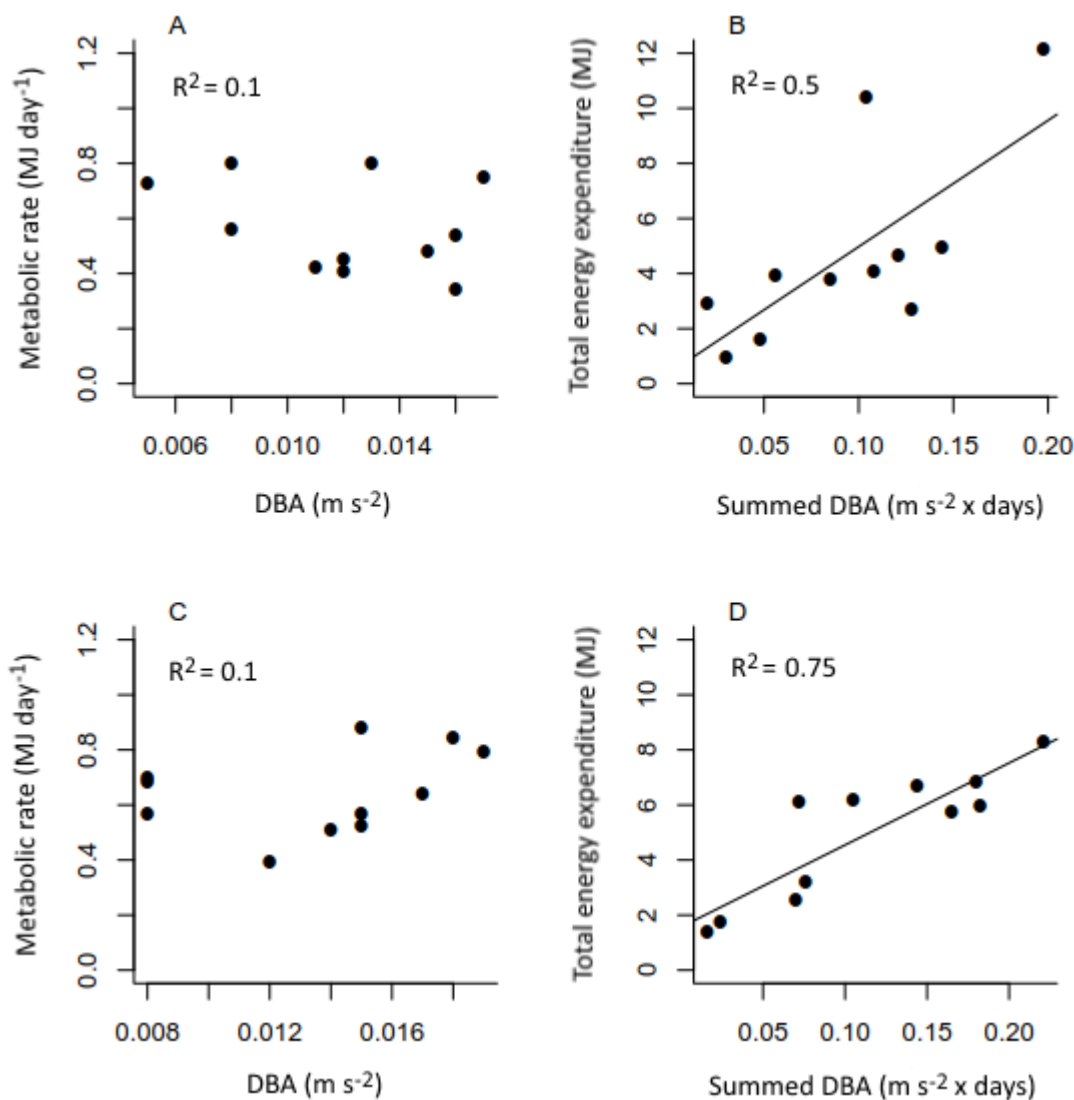
Figure 3. Examples of the simulated relationships between energy expenditure and dynamic body acceleration (DBA) produced by the model, where R2 increases considerably when these two variables are multiplied by time. (a) and (c) Relationships between metabolic rate (MJ d^{-1}) and mean DBA, where the values for each variable were randomly generated within pre-set upper and lower bounds. (b) and (d) Relationships between the product of metabolic rate and time (total energy expenditure), and the product of DBA and time (summed DBA), where the values of metabolic rate and mean DBA were those generated to create the relationships presented in (a) and (c) respectively, and the values of time associated with each data point were unique and ranged between pre-set upper and lower bounds. See main text for further details. In (a) and (b) the R^2 values for each relationship (a: R^2 = 0.10; b: R^2 = 0.50) are very close to the mean and modal R^2 values from 10 000 iterations of the model. Panels (c) and (d) show a more extreme scenario but one that still occurred quite frequently, in which R^2 for (a) the relationship between metabolic rate and mean DBA was again 0.10 however (b) the R^2 for the relationship between total energy expenditure and time, and summed DBA, was 0.75.

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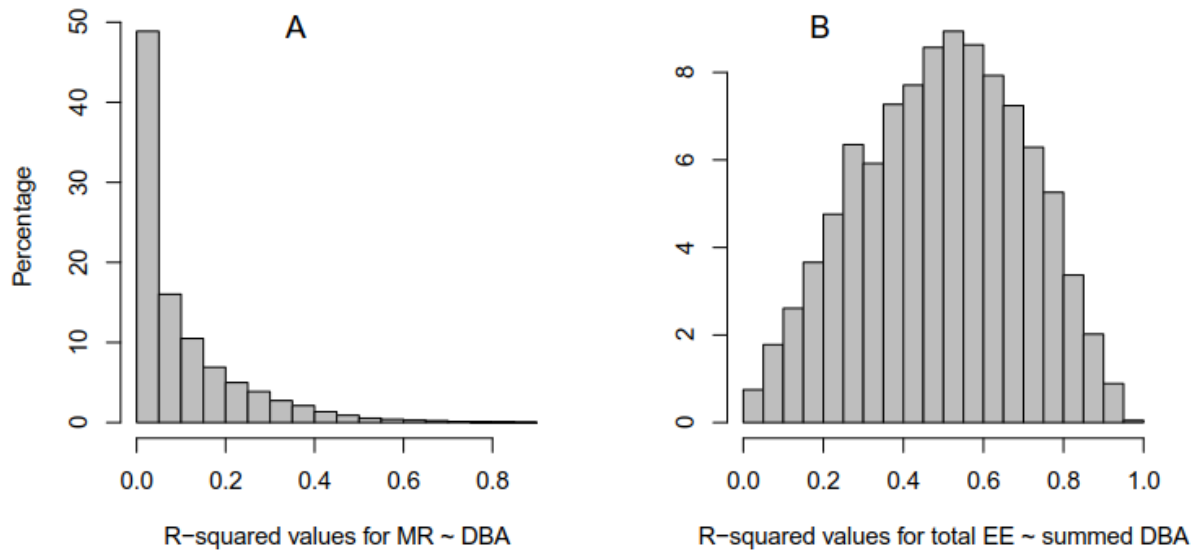
Figure 4. The percentages of binned R^2 values between 0 and 1 for 10 000 iterations of a modelled linear relationship between (a) metabolic rate (MR) and mean dynamic body acceleration (DBA), and (b) summed MR (total energy expenditure; total EE), and summed DBA. See the main text for details.

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