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Accelerometry predicts daily energy expenditure in a bird with high activity levels

Kyle H. Elliott[1], Maryline Le Vaillant[2,3,†], Akiko Kato[2,3], John R. Speakman[4,5] and Yan Ropert-Coudert[2,3]

[1]Department of Biological Sciences, University of Manitoba, Winnipeg, Canada R3T 2N2
[2]Université de Strasbourg, IPHC, 23 rue Becquerel 67087, Strasbourg, France
[3]CNRS, UMR7178, 67087 Strasbourg, France
[4]Institute of Environmental and Biological Sciences, University of Aberdeen, Aberdeen, UK
[5]Key State Laboratory of Molecular Development, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, China

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Author for correspondence:
Kyle H. Elliott
e-mail: urialomvia@gmail.com

†Present address: Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden.

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Animal ecology is shaped by energy costs, yet it is difficult to measure fine-scale energy expenditure in the wild. Because metabolism is often closely correlated with mechanical work, accelerometers have the potential to provide detailed information on energy expenditure of wild animals over fine temporal scales. Nonetheless, accelerometry needs to be validated on wild animals, especially across different locomotory modes. We merged data collected on 20 thick-billed murres (*Uria lomvia*) from miniature accelerometers with measurements of daily energy expenditure over 24 h using doubly labelled water. Across three different locomotory modes (swimming, flying and movement on land), dynamic body acceleration was a good predictor of daily energy expenditure as measured independently by doubly labelled water ($R^2 = 0.73$). The most parsimonious model suggested that different equations were needed to predict energy expenditure from accelerometry for flying than for surface swimming or activity on land ($R^2 = 0.81$). Our results demonstrate that accelerometers can provide an accurate integrated measure of energy expenditure in wild animals using many different locomotory modes.

1. Introduction

Energy costs relative to energy intake determine many aspects of animal ecology, including behavioural decisions, timing of reproduction and, ultimately, mortality. Nonetheless, animal ecologists have developed only a handful of methods for measuring energy costs in the wild. The doubly labelled water method provides only a single, time-averaged value [1]. Heart-rate methods provide values at fine temporal scales, but often involve surgery and can be influenced by cardiovascular adjustments that do not affect energy expenditure [2,3].

The miniaturization of electronic loggers has allowed for the development of tiny accelerometers, which can be attached without surgery [4–6]. Because the dynamic component of body acceleration should be a robust index of mechanical power output for a known body mass, accelerometers can, in theory, provide an index of nearly instantaneous energy expenditure [7]. Accelerometers have the potential to measure variation in the costs of fine-scale behaviours (preening, fighting and sprints) that are not captured by simple time budget models [7]. However, mechanical power in homeotherms is usually only 15–25% of energy costs, and oxygen consumption rates can be only loosely related to mechanical power because of variability in muscle efficiency and other factors [8,9]. In particular, muscle efficiency may vary across locomotory modes; the relative difference in average body acceleration between flying and swimming in cormorants was less than the relative difference in estimated metabolism during flying and swimming [10]. Therefore, the

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relationship between metabolic rate and accelerometry in one locomotory mode is not necessarily valid in another mode, and predictions of the cost of flying or diving based on validations of animals running on treadmills may not be accurate [3].

It is, therefore, important to validate the principle that acceleration can be used to generate measures of energy expenditure on free-living animals. In particular, it is important to validate that the calibration(s) of acceleration to determine energy expenditure hold(s) across different locomotory modes, temperatures and other vagaries present in the wild environment. Such validations have been accomplished on humans [11–13] and many different animals in captivity [3,7,9,14], including pinnipeds freely diving at isolated ice holes or trained to surface into respirometry chambers [5,15].

We attached accelerometers for 24 h to wild thick-billed murres (*Uria lomvia*) regularly swimming in −2°C to 8°C water and flying and moving on land in 8°C to 18°C air. We simultaneously measured daily energy expenditure using doubly labelled water. We predicted that dynamic body acceleration strongly correlates with energy expenditure, but depends on locomotory mode.

2. Material and methods

We captured 20 breeding (four incubating, 16 chick rearing) thick-billed murres at the Coats Island colony, Nunavut, Canada, in 2009. Over 24 h, we simultaneously measured daily energy expenditure using doubly labelled water, acceleration at 16 Hz using an accelerometer (M190-D2GT, Little Leonardo, Tokyo, Japan), and time spent flying, swimming and moving on land (see the electronic supplementary material for isotope measurements, conversion equations, past validations for doubly labelled water, details on logger attachment and determination of time budgets). We converted the measured acceleration data to partial dynamic body acceleration (PDBA), a putative measure of energy expenditure that removes the static component of acceleration associated with posture via smoothing (see the electronic supplementary material).

All isotopic measurements were conducted by a technician in the University of Aberdeen laboratory, who was blind to the accelerometry results. All PDBA results were obtained from a computer script originally developed for a separate bird species and run by a co-author (A.K.) who was blind to the doubly labelled water measurements.

We used R 2.10.1 to estimate calibration coefficients that minimized the log-likelihood of a particular general linear model describing daily energy expenditure (dependent variable) from dynamic acceleration (independent variable), and used Akaike's information criterion (AIC) to compare among models, as AIC penalizes models that are needlessly complex. We compared models with separate calibration coefficients for each locomotory mode with models that had a single calibration coefficient that applied across all locomotory modes. We considered the null model to be a model using time budget alone (model 1, such as time spent flying) and compared that model with the model with dynamic acceleration (model 2, such as acceleration during flight). In either case, the AIC would select the more parsimonious, simplified model for describing daily energy expenditure as a function of time budgets or accelerometry.

3. Results

Average PDBA for an individual was positively correlated with daily energy expenditure ($R^2 = 0.73$, $t_{19} = 6.77$, $p < 0.0001$; figure 1*a*,*b*). Accelerometry (the product of the average value of PDBA for each individual for each locomotory mode and time during that mode) was consistently better than time budgets alone in predicting field metabolic rate (table 1). The most parsimonious models considered modes at the water surface and on land to have similar calibration coefficients, with models further separating out flight and diving to be almost equally parsimonious (table 1). Adding average temperature or mass across the accelerometer deployment as a parameter did not improve the AIC values (table 1).

4. Discussion

Dynamic body acceleration closely predicted field metabolic rate, measured independently via doubly labelled water, in wild birds using three different locomotory modes (flying, swimming and movement on land) in an environment that included diving into sub-zero water. Thus, despite the confounding effects of environmental noise such as wave action, potential movement in the third axis of motion, thermoregulation, digestion and variability in muscle efficiency among media, biaxial accelerometry provided a reliable index of overall energy expenditure. Given that there is uncertainty (approx. 10%) at the individual level associated with the doubly labelled water technique [1], which would tend to reduce the strength of correlation, accelerometry may be an even better index of energy expenditure than our measurements suggest. Our R^2 value is above those obtained in captive experiments comparing metabolic rate with overall dynamic body acceleration using respirometery in diving homeotherms ($R^2 = 0.47$ in diving Steller's sea lions, *Eumetopias jubatus* [14]; $R^2 = 0.53$ in diving double-crested cormorants, *Phalacrocorax auritus* (but no relation between average values) [9]), but lower than those measurements obtained for running homeotherms ($R^2 = 0.81$ to 0.94 across 11 birds/mammals on a treadmill, [7,16]). Our correlations are over the natural range of average daily PDBA values and include a single value per individual, whereas the treadmill studies could sustain a wider range of average PDBA values over the shorter timescale of those measurements and include multiple values per individual, increasing the R^2 values. One reason we found a relatively high relationship may be that auks have relatively high locomotory costs [17,18], and, therefore, variation among individuals in other metabolic components (digestion, thermoregulation, cellular processes) is relatively small.

Our results support the conclusions made by Gómez-Laich *et al.* [10], who found that overall dynamic body acceleration was similar between flying and fast walking on a treadmill for cormorants, even though the theoretical model estimated flight costs to be double that of fast walking. The most parsimonious model in our study suggested that the formula relating PDBA to energy expenditure was different for flying and all other locomotory modes, although there was almost identical support for a model that had separate calibration coefficients between PDBA and energy expenditure for flying, diving and resting (table 1). Thus, although PDBA was higher during flying than resting, it was not nearly as high as it should have been were there a linear relationship between PDBA in flying with PDBA in resting (figure 1*a*). The implication that mechanical energy efficiency (the calibration coefficient between PDBA and energy

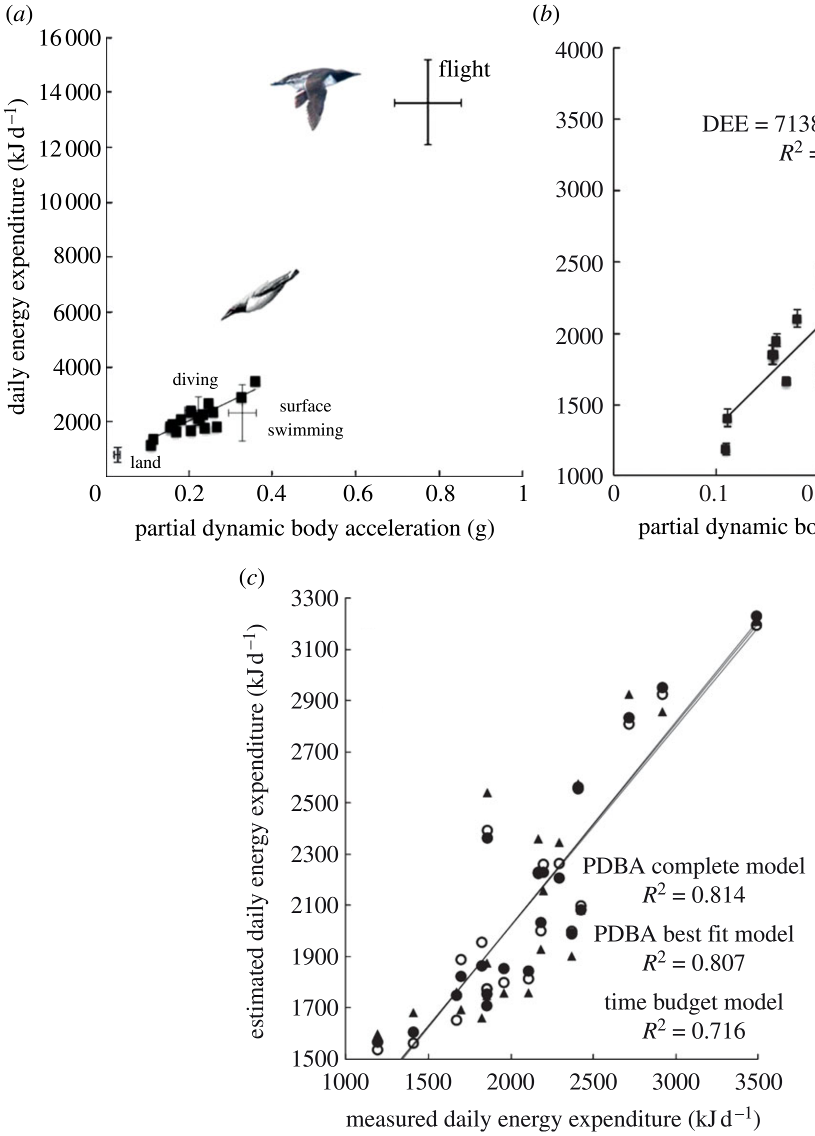

Figure 1. (*a*) Partial dynamic body acceleration (PDBA) reliably predicts daily energy expenditure (DEE) in thick-billed murres moving freely across different locomotory modes (walking, swimming and flying; average values for each mode shown). (*b*) Same data with uncertainty in doubly labelled water measurements calculated using a jack-knife approach. Calculations were made using the mean at each point and systematically omitting individual data points. Multiplying the standard deviation of the resulting confidence interval by 1.96 created the estimated uncertainty. (*c*) Models including PDBA (best fit (open circle), lowest AIC model from table 1; complete (filled circle), all four variables parametrized) outperformed time budget models (filled triangle) at predicting daily energy expenditure. Ordinary least-squares regressions overlap and are shown for all three models.

Table 1. Comparisons among models for explaining energy expenditure in wild thick-billed murres during four locomotory modes: flying, diving, surface swimming and movement on land. We considered all potential time budget and partial dynamic body acceleration (PDBA) models. We present all models with ΔAIC < 2, as well as three null models: two different time budget models and the model only including average PDBA across all locomotory modes. Time budget models had no intercept whereas PDBA models had an intercept and therefore included one additonal parameter.

model	ΔAIC	AIC weight
$\text{PDBA}_{\text{flying}} + \text{PDBA}^{\text{a}}_{\text{all other modes}}$	0.00	0.40
$\text{PDBA}_{\text{flying}} + \text{PDBA}_{\text{diving}} + \text{PDBA}_{\text{land and surface}}$	0.01	0.40
$\text{PDBA}_{\text{flying}} + \text{PDBA}_{\text{surface}} + \text{PDBA}_{\text{diving}} + \text{PDBA}_{\text{land}}$	1.65	0.06
$\text{PDBA}_{\text{flying}} + \text{PDBA}_{\text{all other modes}} + \text{temperature}$	1.86	0.05
$\text{PDBA}_{\text{flying}} + \text{PDBA}_{\text{all other modes}} + \text{mass}$	1.94	0.04
$\text{time}_{\text{flying}} + \text{time}_{\text{all other modes}}$	4.39	0.00
$\text{time}_{\text{flying}} + \text{time}_{\text{surface}} + \text{time}_{\text{diving}} + \text{time}_{\text{land}}$	6.14	0.00
$\text{PDBA}_{\text{all modes}}$	9.98	0.00

[a] Equation for most parsimonious model was: daily energy expenditure = $(0.147 \pm 0.024)\ \text{PDBA}_{\text{flying}} + (0.062 \pm 0.019)\ \text{PDBA}_{\text{all other modes}} + (990 \pm 183)$.

expenditure) is similar across most locomotory modes, except flight, supports the idea that minimum transport costs depend on taxonomic group rather than the medium [19], whereas the clearly different mechanical energy efficiency in air compared with water and land supports the idea that minimum transport costs depend primarily on the physical constraints of a particular medium [20].

Accelerometry was not only a good predictor of energy expenditure, it was better than time spent away from the colony, time spent flying, time spent diving or a multiple regression of time spent flying and diving (table 1). Presumably, accelerometry accounted for some of the variation in energy costs within each locomotory mode associated with preening, social interactions, wind speed and dive strategies. For instance, murres actively pursue prey throughout dives directed towards schooling prey and are relatively inactive during the bottom phase of dives directed towards benthic prey [20,21].

Given the strong commercial pressure provided by the presence of accelerometers in smart phones, it is likely that the cost and size of accelerometers will continue to diminish [6]. We are, therefore, entering an era where ecologists can accurately assign energy costs to discrete behaviours during almost instantaneous periods in wild animals.

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References

1. Speakman JR. 1997 *Doubly-labelled water: theory and practice*. London, UK: Chapman and Hall.
2. Green JA. 2011 The heart rate method for estimating metabolic rate: review and recommendations. *Comp. Biochem. Physiol. A* **158**, 287–304. (doi:10.1016/j.cbpa.2010.09.011)
3. Green JA, Halsey LG, Wilson RP, Frappell PB. 2009 Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *J. Exp. Biol.* **212**, 471–482. (doi:10.1242/jeb.026377)
4. Yoda K, Naito Y, Sato K, Takahashi A, Nishikawa J, Ropert-Coudert Y, Kurita M, Le Maho Y. 2001 A new technique for monitoring the behaviour of free-ranging Adélie penguins. *J. Exp. Biol.* **204**, 685–694.
5. Williams TM, Fuiman LA, Horning M, Davis RW. 2004 The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973–982. (doi:10.1242/jeb.00822)
6. Ropert-Coudert Y, Wilson RP. 2005 Trends and perspectives in animal-attached remote-sensing. *Front. Ecol. Environ.* **3**, 437–444. (doi:10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2)
7. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ. 2006 Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081–1090. (doi:10.1111/j.1365-2656.2006.01127.x)
8. Ward S, Möller U, Rayner JMV, Jackson DM, Bilo D, Nachtigall W, Speakman JR. 2001 Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. *J. Exp. Biol.* **204**, 3311–3322.
9. Halsey LG, White CR, Enstipp MR, Wilson RP, Butler PJ, Martin GR, Grémillet D, Jones DR. 2011 Assessing the validity of the accelerometry technique for estimating the energy expenditure of diving double-crested cormorants *Phalacrocorax auritus*. *Physiol. Biochem. Zool.* **84**, 230–237. (doi:10.1086/658636)
10. Gómez-Laich A, Wilson RP, Gleiss AC, Shepard ELC, Quintana F. 2011 Use of overall dynamic body acceleration for estimating energy expenditure in cormorants: does locomotion in different media affect relationships? *J. Exp. Mar. Biol. Ecol.* **399**, 151–155. (doi:10.1016/j.jembe.2011.01.008)
11. Plasqui G, Westerterp KR. 2007 Physical activity assessment with accelerometers: an evaluation against doubly labeled water. *Obesity* **15**, 2371–2379. (doi:10.1038/oby.2007.281)
12. Halsey LG, Shepard ELC, Hulston CJ, Venables MC, White CR, Jeukendrup AE, Wilson RP. 2008 Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, *Homo sapiens*. *Zoology* **111**, 231–241. (doi:10.1016/j.zool.2007.07.011)
13. Leenders NY, Sherman WM, Nagaraja HN. 2006 Energy expenditure estimated by accelerometry and doubly labeled water: do they agree? *Med. Sci. Sports Exerc.* **38**, 2165–2172. (doi:10.1249/01.mss.0000235883.94357.95)
14. Enstipp MR, Ciccione S, Gineste B, Milbergue M, Ballorain K, Ropert-Coudert Y, Kato A, Plot V, Georges J-Y. 2011 Energy expenditure of freely swimming adult green turtles (*Chelonia mydas*) and its link with body acceleration. *J. Exp. Biol.* **214**, 4010–4020. (doi:10.1242/jeb.062943)
15. Fahlman A, Wilson R, Svärd C, Rosen DAS, Trites AW. 2008 Activity and diving metabolism correlate in Steller sea lion *Eumetobias jubatus*. *Aquat. Biol.* **2**, 75–84. (doi:10.3354/ab00039)
16. Halsey LG, Shepard ELC, Quintana F, Gomez-Laich A, Green JA, Wilson RP. 2009 The relationship between oxygen consumption and body acceleration in a range of species. *Comp. Biochem. Physiol. A* **152**, 197–202. (doi:10.1016/j.cbpa.2008.09.021)
17. Roby DD, Ricklefs RE. 1986 Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. *Physiol. Zool.* **59**, 661–678.
18. Sato K *et al*. 2007 Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. B* **274**, 471–477. (doi:10.1098/rspb.2006.0005)
19. Williams TM. 1999 The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Phil. Trans. R. Soc. Lond. B* **354**, 193–201. (doi:10.1098/rstb.1999.0371)
20. Schmidt-Nielsen K. 1972 Energy cost of swimming, flying and running. *Science* **177**, 222–228. (doi:10.1126/science.177.4045.222)
21. Elliott KH, Woo K, Benvenuti S. 2009 Do activity costs determine foraging tactics for an arctic seabird? *Mar. Biol.* **156**, 1809–1816. (doi:10.1007/s00227-009-1214-1)
22. Elliott KH, Davoren GK, Gaston AJ. 2008 Time allocation by a deep-diving bird reflects prey type and energy gain. *Anim. Behav.* **75**, 1301–1310. (doi:10.1016/j.anbehav.2007.09.024)