

## RESEARCH ARTICLE

# Accelerating animal energetics: high dive costs in a small seabird disrupt the dynamic body acceleration–energy expenditure relationship

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## ABSTRACT

Accelerometry has been widely used to estimate energy expenditure in a broad array of terrestrial and aquatic species. However, a recent reappraisal of the method showed that relationships between dynamic body acceleration (DBA) and energy expenditure weaken as the proportion of non-mechanical costs increases. Aquatic air breathing species often exemplify this pattern, as buoyancy, thermoregulation and other physiological mechanisms disproportionately affect oxygen consumption during dives. Combining biologging with the doubly labelled water method, we simultaneously recorded daily energy expenditure (DEE) and triaxial acceleration in one of the world's smallest wing-propelled breath-hold divers, the dovekie (*Alle alle*). These data were used to estimate the activity-specific costs of flying and diving and to test whether overall dynamic body acceleration (ODBA) is a reliable predictor of DEE in this abundant seabird. Average DEE for chick-rearing dovekies was  $604 \pm 119$  kJ day<sup>-1</sup> across both sampling years. Despite recording lower stroke frequencies for diving than for flying (in line with allometric predictions for auks), dive costs were estimated to surpass flight costs in our sample of birds (flying: 7.24× basal metabolic rate, BMR; diving: 9.37× BMR). As expected, ODBA was not an effective predictor of DEE in this species. However, accelerometer-derived time budgets did accurately estimate DEE in dovekies. This work represents an empirical example of how the apparent energetic costs of buoyancy and thermoregulation limit the effectiveness of ODBA as the sole predictor of overall energy expenditure in small shallow-diving endotherms.

**KEY WORDS:** Accelerometer, Arctic, Ecology, Metabolism

## INTRODUCTION

Energy is the most important currency in animal ecology, influencing behavioural decisions, the timing of reproduction and, ultimately,

fitness (Brown et al., 2004; Grémillet et al., 2018). Nonetheless, animal ecologists have developed only a handful of methods for estimating energy costs in the wild, all having strengths and weaknesses (Fort et al., 2011). For example, the doubly labelled water (DLW) method provides only a single accurate, time-averaged value (Speakman, 1997). 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 (Butler et al., 2004; Green, 2011). In the past two decades, accelerometry has become a popular tool for estimating energy expenditure in wild animals (Elliott, 2016; Wilson et al., 2006), though its origins date back to the early 1960s when laboratory studies began validating the technique in humans (Cavagna et al., 1963; Halsey et al., 2011b). 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, assuming that mechanical power is a constant proportion of total energy costs (Wilson et al., 2006). Indeed, studies on several animal taxa have shown the effectiveness of accelerometers as tools for accurately estimating activity-specific energetic costs (Elliott et al., 2013a; Halsey et al., 2011a; Lear et al., 2017; Murchie et al., 2011). Although observation-based time budgets have provided rough estimates of activity costs, accelerometers are capable of recording activity in greater detail and do not require constant visual contact by observers (Halsey et al., 2011a; Wilson et al., 2006). While other biologgers such as time–depth–temperature tags can also help estimate energy costs in some species, they are often less effective than accelerometers at identifying certain behaviours (Elliott and Gaston, 2014). Furthermore, the continued miniaturization of technology means biologists are able to equip smaller and smaller organisms with accelerometers.

While dynamic body acceleration (DBA) is undoubtedly a revolutionary advance in the field of wildlife energetics, the nearly two decades of study in a wide variety of species has revealed a few weaknesses with its use as the sole predictor of metabolic rate in some animals. In a recent reappraisal of DBA's use in energetics modelling, Wilson et al. (2020) demonstrated that high and variable non-locomotory energetic costs, such as those linked to thermoregulation, can sometimes mask the relationship between DBA and metabolic rate. Thermal substitution, or the reduction of thermoregulatory costs linked to residual heat produced by muscles during periods of elevated activity (Lovvorn, 2007), can also significantly change the nature of the DBA–energy expenditure relationship in cold environments (Wilson et al., 2020). Animals moving through different media or relying on more than one method of locomotion provide another potential pitfall for researchers attempting to correlate overall energy expenditure with DBA. For example, a similar recording of DBA in air and in water could result

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in very different energy expenditures for an animal moving in both aerial and aquatic habitats. This difference is also exacerbated when movement in each medium results from different locomotory mechanisms. Hence, some behaviours may disproportionately affect recorded DBA without a coincident change in energy use (Wilson et al., 2020). Therefore, DBA's relationship with energy expenditure can be variable, often requiring context- or activity-specific assessment (Elliott et al., 2013b; Elliott, 2016).

For the reasons outlined above, modelling the energetics of breath-hold divers such as seals, turtles and seabirds using DBA has been particularly challenging (Grémillet et al., 2018; Halsey et al., 2011b,c). Notably, dive costs tend to increase non-linearly with lower oxygen consumption rates near the end of long dives as individuals suppress non-essential functions, reduce core temperature and shunt blood directly to arteries (Elliott et al., 2013b; Halsey et al., 2011c; Meir et al., 2008; Niizuma et al., 2007). Additionally, oxygen consumption at the level of the muscle and respiratory system is uncoupled in time during dives (Butler, 2006). Thus, although DBA accurately predicts energy expenditure in flying and running animals (Bishop et al., 2015; Halsey et al., 2011a; Wilson et al., 2006), relationships in diving marine vertebrates are often weak without the addition of other model parameters (Halsey, 2017; Rosen et al., 2017; Wilson et al., 2020). A number of studies on diving seabirds have shown that accelerometers can predict costs remarkably well in the wild (Elliott et al., 2013a,b; Hicks et al., 2017, 2020; Stothart et al., 2016; Sutton et al., 2021). However, several of these studies were focused on flightless species, while others were on relatively large (>1 kg), deep-diving species where thermoregulatory and other non-mechanical dive costs may be straightforward to model. For instance, in one species, the fit was better when dive costs were modelled to decrease exponentially with dive duration (Elliott et al., 2013b). Conversely, the dive energetics of small seabirds are likely to be especially difficult to model using DBA, because of the variable mechanical costs associated with buoyancy and their large surface area to volume ratio leading to particularly high thermoregulatory costs when diving in cold water (Gabrielsen et al., 1991; Lovvorn and Jones, 1991; Lovvorn et al., 2004; Wilson et al., 1992).

Dovekies [or little auks, *Alle alle* (Linnaeus 1758)] are small Arctic-breeding seabirds in the family Alcidae. Their abundance makes them key components of many Arctic ecosystems, both as ecosystem engineers and as prey for terrestrial and avian predators (Burnham and Burnham, 2005; González-Bergonzoni et al., 2017). As one of the smallest diving marine endotherms (only the *Aethia* auklets and *Pelecanoides* diving petrels are slightly smaller), dovekies are also an important species from an energetic standpoint, and though their metabolism has been studied in the past, the specific energetic costs of flying and diving remain unknown (Gabrielsen et al., 1991; Harding et al., 2009a,b; Welcker et al., 2009). Dovekies are diving seabirds that feed on a variety of zooplankton, including fish larvae, euphausiids and their primary prey, copepods (Fort et al., 2010). Given that the ranges of their preferred prey, *Calanus glacialis*, *Calanus finmarchicus* and *Calanus hyperboreus*, are shifting northward as a result of climate change (Beaugrand et al., 2009), dovekies will likely have to switch to a less nutritious species or increase foraging effort, both of which may increase daily energy expenditure (DEE) (Amélineau et al., 2016; Grémillet et al., 2012). So far, dovekies have shown a remarkable resilience to the shift, but their ability to buffer its effects may be reaching its limit (Amélineau et al., 2019; Grémillet et al., 2012; Harding et al., 2009b). Understanding dovekie energetics is

key to forecasting their current and future responses to global change (Clairbaux et al., 2021).

In this context, we tested whether accelerometers could estimate activity-specific energetic costs in this small breath-hold diving species. We estimated the energetic costs of flying and diving in dovekies using both time-averaged energy expenditure, obtained using the DLW method, and individual activity profiles, derived from triaxial acceleration data. We expected dovekie dive costs to be higher than in other auk species as a result of the high buoyancy and thermoregulatory costs for small, shallow-diving seabirds. In agreement with the current literature, we also expected these higher non-mechanical costs to weaken the overall relationship between DBA and energy expenditure in this species. As stroke frequency coincides directly with the power generated by the contraction of muscle fibres in animals that swim and/or fly (Pennycuik, 2008), we expanded on previous allometric analyses of stroke frequency across species to further assess whether high dive costs in dovekies could be explained by mechanical costs alone, or whether other non-locomotory factors are at play.

## MATERIALS AND METHODS

### Study area and data collection

Dovekies were studied at Ukaleqarteq (Kap Höegh), East Greenland (70°43'N, 21°33'W) during the 2017 and 2018 breeding seasons. In total, 89 individuals (35 in 2017 and 54 in 2018) were captured using a variety of methods including noose carpets and lassos placed on the rocks surrounding their nests. Each dovekie was injected intraperitoneally with 0.3 ml (2017) or 0.45 ml (2018) of DLW (the dosage was increased in 2018 to extend the recapture window; Speakman, 1997). We taped small triaxial accelerometers (Axy4, Technosmart, Italy; 3.4 g including tubing and tape) to the breast feathers of 60 of these birds to record their activity. Recapture began approximately 20 h after the birds were released. Body measurements (flattened wing, tarsus and beak length) were taken for each dovekie following final blood sampling. While all the data pertaining to dovekies were collected by the authors here, stroke frequency data for other vertebrate species were acquired from published research by Sato et al. (2007) and Elliott et al. (2004).

### Energy expenditure

To estimate the average energy expenditure of each of our birds, we used the DLW method (Speakman, 1997; Welcker et al., 2009). This method estimates carbon dioxide production using the differential decline of heavy isotopes of hydrogen and oxygen in the body. The two-sample approach involves taking a blood sample at the beginning and at the end of a measurement period, while the one-sample approach involves taking only a final sample and interpolating the initial enrichment of <sup>18</sup>oxygen and deuterium. We used the one-sample method for all our accelerometer-equipped birds to reduce handling time (handling time: ~10–15 min). The increased handling time associated with the two-sample approach is known to alter behaviour, and therefore energy expenditure, in other seabirds (Schultner et al., 2010). As such, the two-sample approach was reserved for those birds that were not equipped with accelerometers and whose initial isotope enrichment could be used to interpolate the initial enrichment of the one-sample birds using body mass ( $R^2=0.68-0.74$  between isotopes and mass depending on year; Fig. S1, see Supplementary Materials and Methods).

Immediately following capture, all birds were weighed in an opaque breathable bag using a small hanging scale and then injected intraperitoneally with DLW (65% H<sub>2</sub>O<sup>18</sup>; 35% D<sub>2</sub>O). The one-sample birds were equipped with an accelerometer, marked with dye

and then released. Following the DLW injection, we placed the two-sample birds in the shade for 1 h to allow the DLW to equilibrate with the body water. After the hour had elapsed, an initial blood sample was taken from each bird's brachial vein, following which the birds were marked with dye and released. All birds were recaptured for a final weighing and blood sample after 15–50 h (accelerometers were removed prior to weighing). The isotopic enrichment of blood samples was measured using an isotopic water analyser (Los Gatos, San Jose, CA, USA). We calculated the amount of carbon dioxide produced by individuals over the course of each deployment using the plateau method (see Speakman, 1997, for details on calculations and supporting theory). To estimate energy expenditure, we converted these values into kilojoules using a conversion coefficient of  $27.97 \text{ J ml}^{-1}$  of  $\text{CO}_2$  (Welcker et al., 2009). DEE was then estimated by dividing total energy expenditure by the deployment duration for each dovekie. An unbalanced two-way ANOVA was performed using the car package in R (Fox and Weisberg, 2019) to test for differences in mean DEE estimated for dovekies across sampling years and DLW sampling approaches (i.e. one- and two-sample). Normality and homogeneity of variance were assessed visually using standard residual plots ( $Q-Q$  plot and residuals versus fitted plot).

### Accelerometry and activity costs

Raw acceleration data in the surge, heave and sway axes were recorded at a sampling rate of 50 Hz and used to calculate stroke frequency and pitch (i.e. body angle) in R using code adapted from Patterson et al.'s (2019) work on thick-billed murrelets. Specifically, a fast Fourier transform, applied over a 5 s moving window, was used to determine the peak frequency in the heave axis (Patterson et al., 2019). Flights were identified as any period with a stroke frequency greater than 10 Hz. Pitch was calculated using a 2 s moving average of the heave, sway and surge axes. To account for differences among individuals and the placement of accelerometers on birds, pitch values were standardized to 0 during flights (Patterson et al., 2019). A 3 s moving window of pitch was used to define periods when the dovekie was descending (pitch  $< -45$  deg) or ascending (pitch  $> 45$  deg).

As we did not have a pressure sensor, the start of likely dives was determined based on periods when the dovekie was descending for at least 2 s, with a stroke frequency between 1 and 6 Hz. During the bottom phase of a dive, the dovekie uses either dive strokes or changes in pitch to maintain buoyancy and search for prey. From the start of a likely dive, we identified the next time when the bird was not ascending or descending, did not have a stroke frequency between 1 and 6 Hz, and had a change in pitch of less than 10 deg (i.e. when it was assumed to be back at the surface). If these conditions were not met within 120 s (the presumed maximum dive duration), then the end of the dive was defined as 120 s after the dive start. These diving periods were also identified visually in a subset of deployments in order to verify the validity of the automatic classifications and were found to be in close agreement (Cohen's kappa coefficient =  $0.82 \pm 0.08$ ,  $n=10$ ). As such, only automatically defined dives were used in all further analyses. Automatic dive classification R-code is available in the Supplementary Materials and Methods.

To estimate energetic costs in dovekies, we compared several models using activity-specific time budgets and DBA as predictors. We began by conducting multiple regression analyses with activity-specific time budgets (percentage of total deployment time) as explanatory variable and mass-specific DEE as the response variable. We opted to use mass-specific DEE instead of absolute

DEE to facilitate comparisons with the DBA models described in the next section (further justification is given in the Supplementary Materials and Methods, Fig. S2). As one of the primary objectives of the study was to estimate flight and dive costs, three activity categories were initially selected for analysis: flying, diving and other (resting, walking, etc.); Model 1:

$$\text{DEE} = a(\% \text{Time}_{\text{fly}}) + b(\% \text{Time}_{\text{dive}}) + c(\% \text{Time}_{\text{other}}). \quad (1)$$

The intercept was forced through zero to account for the fact that no energy is expended when no time has elapsed (this also applies to the other time budget models described below). The output of the multiple regression analysis was then used to estimate the activity-specific costs of flying and diving in dovekies.

Other model variants were subsequently tested against our basic model to see which best explained DEE. Several variants used combinations of the basic time budget categories outlined above as explanatory variables (Models 2–4), while another split the 'other' category into 'resting on land' and 'unknown' (Model 5; details available in the Supplementary Materials and Methods). Unfortunately, we could not further breakdown the 'unknown' category into other potentially important behaviours using acceleration data only, a limitation of working with such a small species where larger tags cause behavioural disruption. As dive costs could have declined exponentially with dive duration (e.g. Elliott et al., 2013b), as measured in penguins and modelled in larger auks, we also tested a model variant that replaced the percentage of time spent diving with an exponential cost function for each dive (Model 6; details available in the Supplementary Materials and Methods). We then considered models incorporating overall dynamic body acceleration (ODBA) as a possible predictor of DEE. ODBA represents the summed dynamic acceleration across all three axes of movement. Dynamic acceleration was calculated by subtracting the static component of acceleration (i.e. that associated with gravity and body position) from the raw acceleration for each axis. Static acceleration was calculated by applying a 2 s rolling mean to the raw acceleration data in order to remove any signal resulting from the animal's movement (e.g. wingbeats). As the effect of time on summed ODBA inflates its importance in energetics models (Halsey, 2017), the first ODBA model variant (Model 7) used overall time-averaged ODBA as the sole explanatory variable. The second ODBA model variant (Model 8) multiplied mean activity-specific ODBA by the time budget percentages for each behavioural category to see whether incorporating ODBA improved the fit of the basic time budget model (i.e. Model 1); Model 8:

$$\text{DEE} = d(\% \text{Time}_{\text{fly}} \times \text{ODBA}_{\text{fly}}) + e(\% \text{Time}_{\text{dive}} \times \text{ODBA}_{\text{dive}}) + f(\% \text{Time}_{\text{other}} \times \text{ODBA}_{\text{other}}). \quad (2)$$

We selected the best model(s) using Akaike's information criterion (AIC), which penalizes unnecessarily complex models (Table 1). The model with the lowest AIC score was considered best, and models with a  $\Delta\text{AIC} < 2$  were assumed to be equivalent to the best model and are discussed in further detail below (Symonds and Moussalli, 2011). Using the coefficients resulting from selected models, we calculated predicted DEE and plotted it against DLW-derived DEE ( $\text{DEE}_{\text{DLW}}$ ). We then performed a reduced major axis (RMA) regression using the *smatr* package for R (Warton et al., 2012) to check whether the predicted DEE was in close agreement with the  $\text{DEE}_{\text{DLW}}$  estimates that our models were based on. To illustrate the potential relationship between DEE and ODBA (i.e. Model 7),  $\text{DEE}_{\text{DLW}}$  was plotted against mean ODBA, revealing an



**Table 1.**  $\Delta$ AIC comparison of time budget ( $n=6$ ) and ODBA ( $n=2$ ) models used to explain doubly-labelled water estimates of mass-specific daily energy expenditure ( $DEE_{DLW}$ ) in doves equipped with accelerometers ( $n=13$ )

Model no.	Model description	$\Delta$ AIC	Weight
2	%Time <sub>fly+dive</sub> +%Time <sub>other</sub>	0.00	0.48
1	%Time <sub>fly</sub> +%Time <sub>dive</sub> +%Time <sub>other</sub>	0.47	0.38
5	%Time <sub>fly</sub> +%Time <sub>dive</sub> +%Time <sub>rest</sub> +%Time <sub>unknown</sub>	2.36	0.15
3	%Time <sub>dive</sub> +%Time <sub>other+fly</sub>	12.51	0.00
6	%Time <sub>fly</sub> + $\Sigma(1-e^{-duration/19.68})$ +%Time <sub>other</sub>	12.98	0.00
8	%Time <sub>fly</sub> $\times$ ODBA <sub>fly</sub> +%Time <sub>dive</sub> $\times$ ODBA <sub>dive</sub> +%Time <sub>other</sub> $\times$ ODBA <sub>other</sub>	13.54	0.00
4	%Time <sub>fly</sub> +%Time <sub>other+dive</sub>	14.70	0.00
7	ODBA <sub>mean</sub>	17.62	0.00

Akaike information criterion (AIC) weights are presented alongside  $\Delta$ AIC values.

obvious gap between points for doves tagged in 2017 and those tagged in 2018. As sampling year could have influenced the relationship between mean ODBA and  $DEE_{DLW}$ , we subsequently conducted a linear regression analysis on both the pooled dataset (2017 and 2018, Model 7) and the dataset for doves tagged in 2017 only. We did not analyse the 2018 dataset independently given the small sample size for that year. Differences in mean ODBA across our three basic behaviour categories (flight, diving and other) were assessed using a one-way ANOVA followed by a Tukey *post hoc* test. Given the small sample size for each test group, residual plots ( $Q-Q$  and residuals versus fitted) were used to check the normality and homogeneity of variance assumptions instead of a formal test. All statistical analyses were conducted in R (<http://www.R-project.org/>).

### Allometry of stroke frequency

Density plots were used to identify the dominant stroke frequency exhibited by individuals during locomotion in the air and underwater. We then tested for an intra-specific linear relationship between  $\log_{10}(\text{stroke frequency})$  and  $\log_{10}(\text{mass})$  in doves while flying and diving. In an attempt to explain some of the residual variation surrounding these relationships, we regressed residuals against wing loading, which was calculated for each bird by dividing their mass by the area of their wings (approximated by wing length squared). We continued to plot the mean dominant stroke frequency observed across all sampled individuals with literature values for other vertebrates (Sato et al., 2007), as well as for Alcids specifically (Elliott et al., 2004). If a species was represented in both studies, we chose the value provided in Sato et al. (2007), which relied on accelerometer-derived estimates instead of video analysis (literature values presented in Table S1).

We then conducted a linear regression analysis on  $\log_{10}$ -transformed mass and stroke frequency to derive inter-specific allometric scaling relationships for stroke frequency in diving and flying Alcids and compared them with those published by Elliott et al. (2004) and Sato et al. (2007) for Alcids and marine vertebrates, respectively.

### RESULTS

Because of weather and logistics constraints, 54% of the 35 deployed doves were recaptured in 2017 and only 31% of the 54 birds deployed in 2018. Of these, several were caught outside the time frame when DLW analysis is possible. We estimated DEE in a total of 24 birds across both sampling years (14 one-sample and 10 two-sample individuals). Of the recaptured individuals for whom DEE could not be estimated, we were able to recover acceleration data from an additional six birds, bringing the total number of recovered accelerometers from one-sample birds to 20. Average  $DEE_{DLW}$  for doves in 2017 and 2018 was  $621 \pm 103$  and  $590 \pm 133$  kJ day<sup>-1</sup>, respectively (Table S2). A two-way ANOVA showed no significant differences between estimates for the two sampling years ( $P=0.90$ ,  $n=11$  in 2017 and  $n=13$  in 2018), or between those for one- and two-sample birds ( $P=0.22$ ,  $n=14$  one-sample and  $n=10$  two-sample).

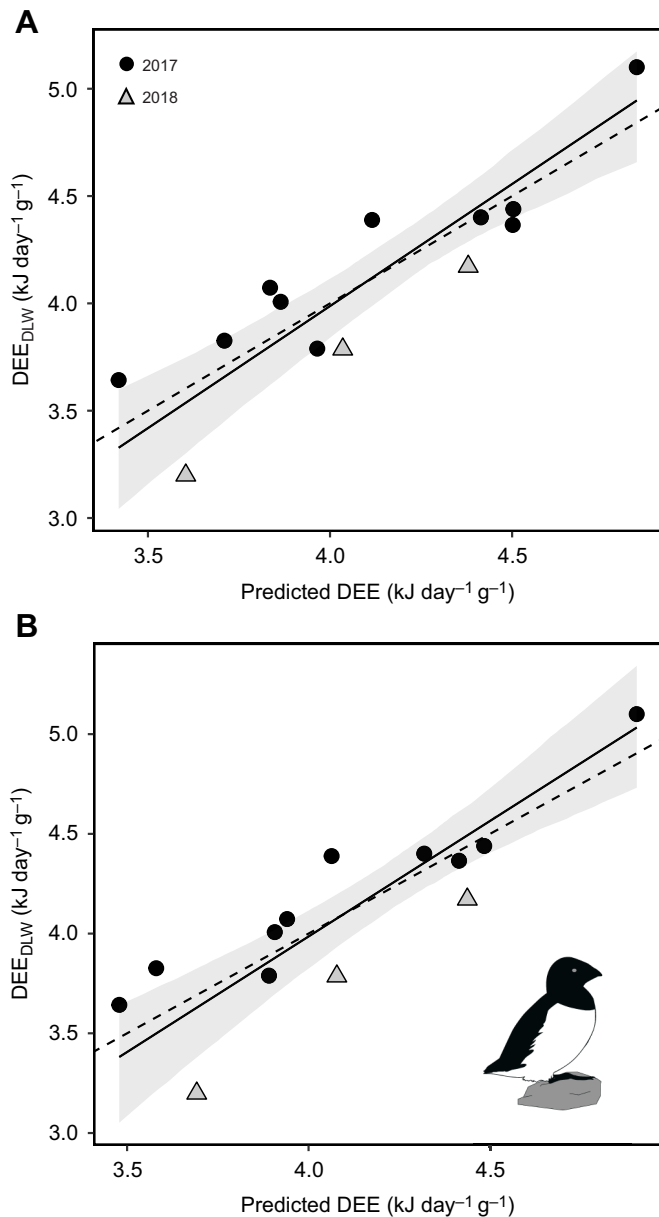
Of the eight model variants used to explain  $DEE_{DLW}$ , two were selected by comparing AIC values, both of which were time budget models (Model 1 and Model 2; Table 1). The coefficients resulting from these models provided energetic cost estimates for each behaviour category (Table 2). From Model 1, the estimated flight cost for doves was  $98$  W kg<sup>-1</sup> (95% confidence interval, CI=63–133 W kg<sup>-1</sup>) or approximately  $7.24 \times$  BMR (using a BMR estimate of  $177.9$  kJ day<sup>-1</sup> for doves of mean mass  $152.5$  g; Gabrielsen et al., 1991). Our estimated dive cost was  $126$  W kg<sup>-1</sup> (95% CI=86–167 W kg<sup>-1</sup>) or approximately  $9.37 \times$  BMR. Model 2, which combined time budgets for flying and diving, estimated a combined cost of  $110$  W kg<sup>-1</sup> (95% CI=86–135 W kg<sup>-1</sup>) for these behaviours (i.e.  $8.16 \times$  BMR). Fig. 1 illustrates the utility of our model coefficients with regards to predicting  $DEE_{DLW}$  (RMA regression with  $n=13$ , Model 1:  $R^2=0.77$ ,  $P=7.48 \times 10^{-5}$ , Fig. 1A; and Model 2:  $R^2=0.74$ ,  $P=0.000145$ , Fig. 1B). Models incorporating ODBA (Models 7 and 8) did not improve on time budget models, nor did replacing the percentage of time spent diving with an exponential cost function (Model 6).

The tagged doves used in our energy expenditure modelling exhibited an overall mean ( $\pm$ s.d.) ODBA of  $0.41 \pm 0.06$  g s<sup>-1</sup>, while activity-specific ODBA was  $0.71 \pm 0.06$  g s<sup>-1</sup> for flight,  $0.67 \pm 0.07$  g s<sup>-1</sup> for diving and  $0.25 \pm 0.08$  for the other behavioural category (Table 3). A one-way ANOVA showed there were significant differences in mean ODBA across behaviours ( $F_{2,36}=167.1$ ,  $P=0.000$ ). A Tukey *post hoc* test revealed that mean

**Table 2.** Output of the best models ( $\Delta$ AIC<2) for explaining  $DEE_{DLW}$  in doves equipped with accelerometers

	Activity cost		
	kJ day <sup>-1</sup> g <sup>-1</sup> *	W kg <sup>-1</sup>	BMR**
%Time <sub>fly+dive</sub>	9.52 (7.40–11.63)	110.1 (85.7–134.6)	8.16 (6.35–9.97)
%Time <sub>other</sub>	0.97 (–0.25–2.19)	11.2 (–2.9–25.4)	0.83 (–0.21–1.88)
%Time <sub>fly</sub>	8.45 (5.44–11.45)	97.8 (63.0–132.5)	7.24 (4.67–9.82)
%Time <sub>dive</sub>	10.93 (7.41–14.45)	126.5 (85.7–167.2)	9.37 (6.35–12.38)
%Time <sub>other</sub>	0.86 (–0.38–2.10)	10.0 (–4.4–24.3)	0.74 (–0.33–1.80)

Estimates are presented with 95% confidence intervals in parentheses. \*As our models used time budget percentages as opposed to proportions, coefficients were multiplied by 100 to get standard units of energy expenditure (i.e. kJ day<sup>-1</sup> g<sup>-1</sup>). \*\*Activity cost estimates presented as multiples of basal metabolic rate (BMR) using a previously published value (BMR=177.9 kJ day<sup>-1</sup>,  $n=16$ , at mean body mass  $152.5$  g; Gabrielsen et al., 1991).

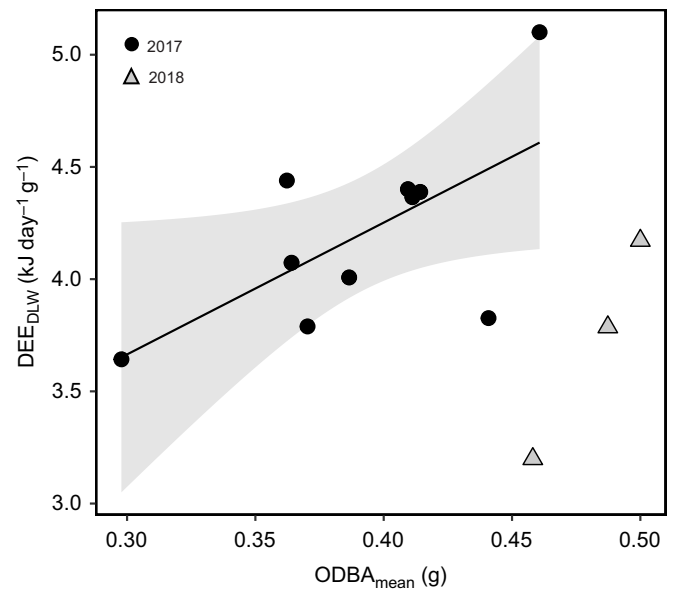


**Fig. 1.** Doubly labelled water (DLW)-derived estimates of daily energy expenditure ( $DEE_{DLW}$ ) plotted against time budget-predicted DEE for the two model variants with  $\Delta AIC < 2$ . (A) Model 1 and (B) Model 2. AIC, Akaike information criterion. Black lines represent the output of a reduced major axis regression with shaded regions depicting 95% confidence interval, CI [ $n=13$ , Model 1:  $R^2=0.77$ ,  $P<0.0001$ ,  $DEE_{DLW}=1.14(\text{predicted DEE})-0.56$ ; Model 2:  $R^2=0.74$ ,  $P<0.001$ ,  $DEE_{DLW}=1.16(\text{predicted DEE})-0.65$ ). Dashed lines depict the lines of equality (i.e. 1:1 relationship).

**Table 3.** Mean and activity-specific time-averaged overall dynamic body acceleration (ODBA) for the accelerometer-tagged dovekies used in our DEE modelling

Year	Time-averaged ODBA ( $\text{g s}^{-1}$ )				<i>n</i>
	Mean	Flying	Diving	Other	
2017	0.39±0.05	0.71±0.07	0.67±0.03	0.22±0.05	10
2018	0.48±0.02	0.71±0.04	0.66±0.17	0.37±0.02	3
Both	0.41±0.06	0.71±0.06	0.67±0.07	0.25±0.08	13

Data are estimates±s.d.



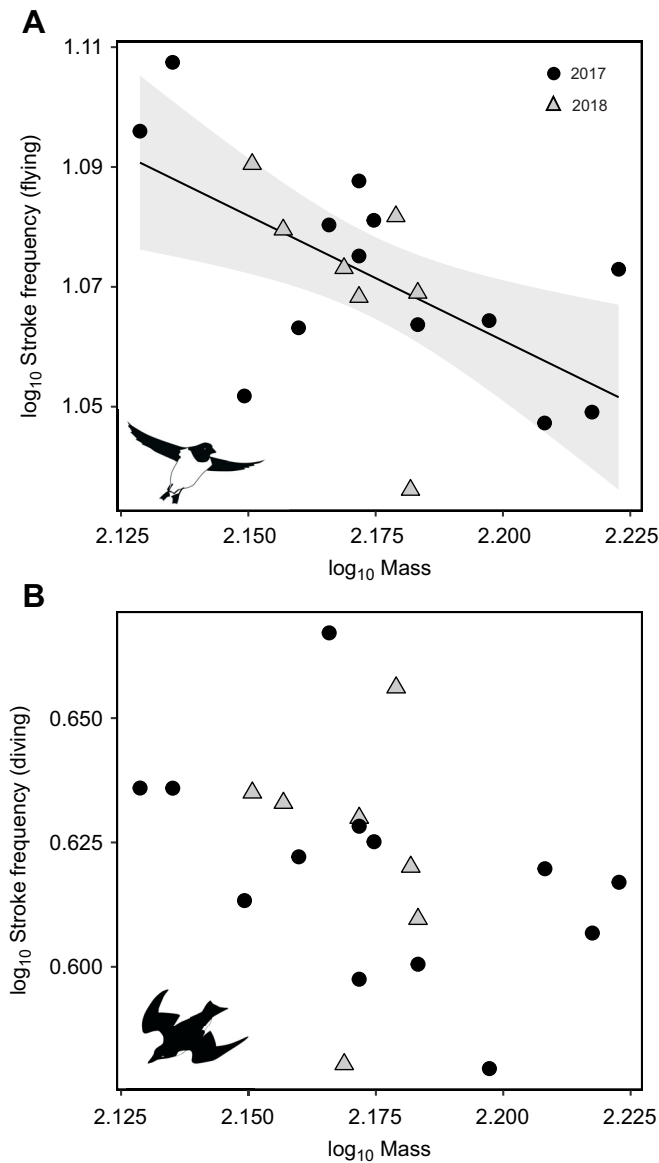
**Fig. 2.**  $DEE_{DLW}$  plotted against time-averaged overall dynamic body acceleration ( $ODBA_{\text{mean}}$ ). There was a weak significant linear relationship between  $DEE_{DLW}$  and  $ODBA_{\text{mean}}$  for dovekies tagged in 2017 ( $R^2=0.41$ ,  $P<0.05$ ,  $n=10$ ;  $DEE_{DLW}=5.87(ODBA_{\text{mean}})+1.90$ ; shaded region represents the 95% CI), but none for the combined datasets of 2017 and 2018 ( $P>0.05$ ,  $n=13$ ).

ODBA during flight and diving was not significantly different from each other ( $P=0.270$ ), but both differed significantly from mean ODBA during ‘other’ behaviours ( $P=0.000$ ). We did not find a significant relationship between DEE and mean ODBA for the 2017 and 2018 pooled dataset ( $P=0.734$ ,  $n=13$ ; Fig. 2). However, a weak linear relationship was found when only using data for dovekies tagged in 2017 ( $R^2=0.41$ ,  $P=0.0478$ ,  $n=10$ ).

Stroke frequency varied significantly with mass across individual dovekies during flight ( $P=0.00641$ ,  $R^2=0.35$ ; Fig. 3A), but not diving ( $P=0.116$ ; Fig. 3B). However, confidence intervals for the allometric exponent for flight were quite broad, indicating a high level of uncertainty surrounding the estimate (exponent= $-0.42$ , 95% CI= $-0.70$  to  $-0.13$ ). Wing loading did not explain residual variation ( $P=0.155$ ). Combining our mean dominant stroke frequency for dovekies with published values for other species of Alcid yielded an allometric scaling exponent of  $-0.22\pm 0.048$  for flight ( $P=0.00176$ ,  $R^2=0.73$ ,  $n=10$ , 95% CI= $-0.33$  to  $-0.11$ ; Fig. 4A), and  $-0.27\pm 0.033$  for diving ( $P=0.00367$ ,  $R^2=0.96$ ,  $n=5$ , 95% CI= $-0.38$  to  $-0.17$ ; Fig. 4B).

## DISCUSSION

In accordance with our expectations for a small shallow-diving endotherm in the Arctic, time-averaged ODBA was not an effective predictor of DEE, though a weak relationship was found when considering data for 2017 only. Similarly, the addition of activity-specific ODBA to basic time budget models did not improve their ability to explain variation in DEE. In fact, our two best models used only accelerometer-derived time budgets as explanatory variables. Despite recording similar ODBA in flying and diving dovekies (Table 3), time budget models suggested the energetic cost of diving could be almost 30% higher than that of flying ( $7.24\times$  BMR for flight and  $9.37\times$  BMR for diving). Put together, these findings suggest that high non-mechanical costs such as thermoregulation during dives weaken the relationship between ODBA and DEE (Wilson et al., 2020). Furthermore, while dive costs were relatively high compared with flight in dovekies, their average stroke

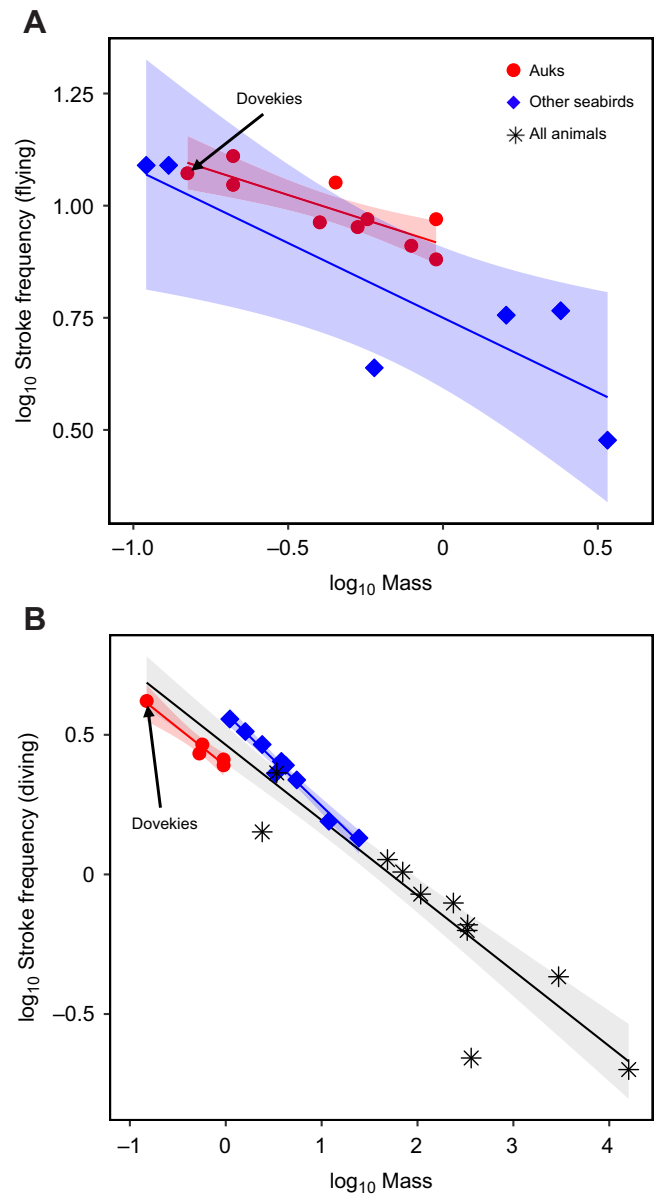


**Fig. 3. Dominant stroke frequency (Hz) plotted against mass (g) for flying and diving dovekeys.** (A) Flying (stroke frequency= $94.914\text{mass}^{-0.416}$ ;  $P < 0.01$ ,  $R^2 = 0.35$ ,  $n = 20$ ) and (B) diving (no significant relationship).

frequency while diving was consistent with inter-species allometric scaling relationships. Thus, dovekeys represent an empirical example of how the link between DBA metrics and energy expenditure is weaker in species apparently facing greater proportions of non-mechanical costs and which exhibit multiple movement modes (Wilson et al., 2020).

### DEE

Despite rapid environmental changes in the Arctic, DEE estimates for nesting dovekeys in 2017 and 2018 in East Greenland were comparable to previous estimates going back ~30 years for birds breeding at the same site and in Svalbard (~600–760 kJ day<sup>-1</sup>; Gabrielsen et al., 1991; Harding et al., 2009b; Welcker et al., 2009). Thermoregulatory energy savings resulting from warming temperatures may be offsetting losses associated with changing foraging dynamics, allowing dovekeys to buffer the effects of climate change in East Greenland (Grémillet et al., 2012). However, as prey dynamics continue to shift with increasing temperatures,



**Fig. 4. Mean stroke frequency (Hz) plotted against mass (kg) for flying and diving animals.** (A) Flying and (B) diving, where the 'All animals' trendline is inclusive of 'auks' and 'other seabirds'. All data points aside from those for dovekeys are derived from previous research by Sato et al. (2007) and Elliott et al. (2004). Stroke frequency varied significantly with mass across auks during flight (stroke frequency= $8.188\text{mass}^{-0.221}$ ;  $P < 0.01$ ,  $R^2 = 0.73$ ,  $n = 8$ ) and while diving (stroke frequency= $2.4453\text{mass}^{-0.274}$ ;  $P < 0.01$ ,  $R^2 = 0.96$ ,  $n = 5$ ). Data for dovekeys are indicated by black arrows.

dovekeys may soon face increased energetic demands that exceed their capacity to buffer, eventually leading to decreases in fitness (Kidawa et al., 2015; Amélineau et al., 2019). As such, it is essential that we continue to monitor the behaviour, energetics and breeding success of these abundant Arctic seabirds. Going forward, the models presented here can be used to easily estimate energy expenditure using basic time budgets derived from accelerometers or other tag types if they can identify periods of flight and diving.

### Activity costs

Until now, only rough estimates of the energetic costs of flying and diving existed for dovekeys and these were based on allometric

relationships or biomechanical modelling (i.e. the Pennycuik model; Pennycuik, 1989). Prior to the availability of fine-scale movement data made possible through the use of accelerometers, diving and flying were estimated in dovekies to cost between  $4.8\times$  and  $11.6\times$  BMR (Fort et al., 2009; Gabrielsen et al., 1991). While both our estimated flight and dive costs fell within that range ( $7.24\times$  and  $9.37\times$  BMR), dive costs were relatively high compared with flight costs. Some species are known to trade-off time budgets for energetically costly behaviours in order to minimize overall costs (Elliott et al., 2013a,b), which may explain why time budgets for flight and diving were negatively correlated across all accelerometer-equipped individuals in our study ( $r=-0.61$ ,  $n=20$ , Fig. S3, see Supplementary Materials and Methods). Regardless, our estimated activity costs can be used to inform our current understanding of the long-term health of dovekie populations globally by improving existing models (e.g. Clairbaux et al., 2019).

The flight costs derived in this study support the idea that high wing loading in dovekies results in high energetic costs during flapping flight. For instance, these estimates are almost double those for the similarly sized sooty tern (*Sterna fuscata*), which has a much lower wing loading than the dovekie (Flint and Nagy, 1984). Even so, when compared with the flight costs of the largest auk species, the thick-billed murre (*Uria lomvia*,  $31\times$  BMR; Elliott et al., 2013b), dovekies have relatively low flight costs. This is almost certainly because thick-billed murres have roughly 2 times higher wing loading than dovekies (Gabrielsen et al., 1991; Elliott et al., 2013b), and induced flight costs increase non-linearly with wing loading [proportional to  $(\text{mass}/\text{wingspan})^2$ ; Pennycuik, 2008]. The effect of mass has been widely studied and, though a level of variability exists, flight costs tend to increase with mass both inter- and intra-specifically in birds (Videler, 2006). This pattern is obvious when comparing the flight costs of one of the smallest Alcids (the dovekie,  $98 \text{ W kg}^{-1}$ ) with those of the largest (the thick-billed murre,  $146 \text{ W kg}^{-1}$ ; Elliott et al., 2013b) but may also be present among individual dovekies of varying mass, though this is beyond the scope of the present study.

As expected, dovekies had relatively high dive costs compared with other species. Though these small seabirds have short dive-adapted wings, they are still longer (relative to body size) than in other Alcids, such as the thick-billed murre, whose relative dive costs are typically lower than in dovekies ( $\sim 40 \text{ W kg}^{-1}$  for an average length dive; Elliott et al., 2013b). Longer wings increase hydrodynamic drag when moving through the water and this translates into increases in the energetic requirements of diving (Elliott et al., 2007). On average, dovekies also exhibit much shorter and shallower dives than thick-billed murres and this likely means that they face much higher costs linked to buoyancy when diving (Elliott et al., 2007; Harding et al., 2009a; Lovvorn et al., 2004). Buoyancy is predicted to decline exponentially with depth and so shallow divers must spend more time and energy overcoming it (Lovvorn et al., 2004; Wilson et al., 1992). Dovekies have been recorded making up to 240 individual dives per day at an average depth of 10 m (Harding et al., 2009a), and so the cost of buoyancy is likely a large contributor to the particularly high dive costs observed in these birds.

Thermoregulatory costs are also likely higher in diving dovekies than in thick-billed murres because of their relatively large surface area to volume ratio (Gabrielsen et al., 1991; Gardner et al., 2011). Small endotherms lose heat much faster in water than in air, leading to significantly higher metabolic rates in water (Croll and McLaren, 1993). These thermoregulatory costs increase steeply as temperatures drop – something that has been demonstrated in many

seabirds resting on water, including three other Alcids (Croll and McLaren, 1993; Richman and Lovvorn, 2011). While thermal substitution can offset some of these costs by recycling heat generated by muscles during dives (Lovvorn, 2007), thermoregulatory costs are likely still high for small Arctic species diving in near-freezing waters. However, as shallow divers (average depth  $\sim 10$  m; Harding et al., 2009b), dovekies may benefit from the air trapped in their feathers whose insulative properties would diminish significantly at greater depth (Lovvorn, 2007). Regardless, the high non-mechanical costs incurred by diving dovekies explains the elevated dive costs predicted here, as well as the decoupling of DBA from energy expenditure observed in these birds (Halsey et al., 2011b; Wilson et al., 2020).

The morphological and physiological characteristics of a species are not the only factors that can influence activity costs. Environmental conditions can also have significant effects on the energetic costs associated with specific behaviours and could explain some of the variation observed in our model. For example, a study undertaken on two species of seabird found that flight costs increased with increasing head winds (Elliott et al., 2014). As such, differences in the wind regimes experienced by the dovekies deployed in 2017 and 2018 could have led to differences in the relative energetic costs associated with flight in each cohort, and previous research on dovekies has shown that DEE increases with wind speed in this species (Gabrielsen et al., 1991). Unfortunately, wind speed could not be measured at the study site during those 2 years. Similarly, interannual differences in sea surface temperature could have affected the thermoregulatory dive costs incurred by dovekies in both sampling years. For example, sea surface temperatures in the colony's foraging range were higher in 2018 (mean for July and August  $1.70\pm 0.39^\circ\text{C}$ ) than in 2017 ( $0.72\pm 0.47^\circ\text{C}$ ), consistent with DEE in 2018 being lower than expected based on activity levels alone (Fig. 1; refer to the Supplementary Materials and Methods for details on how bimonthly mean sea surface temperature was derived).

While estimating activity costs for birds tagged in each year separately could have helped highlight any effects of varying environmental conditions, sample sizes in the present study were too small for this purpose. Given the high thermoregulatory costs predicted for the species, incorporating biologged ambient temperature into energetic models could also improve their predictive power moving forward, especially in light of the rapidly changing environmental conditions faced by dovekies in the Arctic. For example, annual energy expenditure models for the larger common guillemot (*Uria aalge*) showed that DEE was closely linked to biologged temperature in the species (Dunn et al., 2020). However, this may prove challenging for dovekies given additional sensors would increase the weight of tag packages, likely affecting the behaviour and energy expenditure recorded for these small birds (Sun et al., 2020).

### Allometry of stroke frequency

Dominant stroke frequency during flight varied across individual dovekies with  $\text{mass}^{-0.42}$ , higher than the predicted inter- and intra-specific exponent of between  $-1/6$  and  $-1/3$ , but lower than the  $-1/2$  exponent predicted for intra-individual stroke frequency allometry in birds (Berg et al., 2019; Pennycuik, 2008). Inter-individual variation in wingspan and wing area may be relatively small across dovekies, leading to an allometric scaling exponent that approaches  $-1/2$ . This could be the case if mass differences across individuals result from varying fat reserves instead of overall differences in body size (Pennycuik, 2008). While nesting



dovekies may benefit from large fat reserves, they also likely incur higher activity costs associated with increased stroke frequency during flight (Taylor, 1994). However, wing loading did not explain the high degree of variation surrounding the relationship between body mass and stroke frequency in flying dovekies or the lack of a significant relationship for diving dovekies, suggesting other factors are at play here.

We combined the mean stroke frequency of flying and diving dovekies with literature data for other Alcids to assess the inter-specific allometry of stroke frequency in this family with the inclusion of one of its smallest members. Despite Alcids having lower mass-specific stroke frequencies than other swimming vertebrate taxa, the scaling exponent ( $-0.27$ ) obtained for diving Alcids was nearly identical to that observed across birds, fish, reptiles and mammals in a previous study ( $-0.29$ ; Sato et al., 2007; Fig. 4B). This supports the idea that a morphological trade-off between efficient locomotion in air and water affects the intercept and not the slope of log-log relationships for stroke frequency allometry in diving Alcids (Sato et al., 2007). Our estimated allometric exponent for flight in Alcids ( $-0.22$ ) agrees closely with the exponent published by Elliott et al. (2004) despite the addition of data points for three species of Alcid not present in the original dataset. These added species included the largest and smallest studied auks (i.e. the dovekie and the thick-billed murre). Dovekie stroke frequency was well predicted by our derived allometric relationships for flight and diving in Alcids, implying once again that their unusually high dive costs are not driven by mechanical costs alone.

## Conclusion

The use of accelerometers has greatly enhanced our ability to study the fine-scale behaviour and energetics of wildlife. However, our results support the hypothesis that DBA alone is not an effective predictor of DEE in species experiencing high non-mechanical energetic costs and using multiple movement modes (Wilson et al., 2020). Nevertheless, acceleration-derived time budgets were effective at providing estimates of energy expenditure in dovekies, and revealed that dive costs are particularly high in this species. As the DLW method is challenging to perform in species such as dovekies, accelerometers can be used to study their energetics going forward. Additionally, the use of accelerometer-derived information in ecological modelling is not restricted to energetics alone. The detailed data provided by these tags can also be used to parametrize other models forecasting the fitness, distribution and population dynamics of species faced with the mounting pressures of global change (e.g. Grémillet et al., 2018).

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## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: E.S.-M., D.G., J.F., K.H.E.; Methodology: E.S.-M., D.G., K.H.E.; Software: E.S.-M.; Formal analysis: E.S.-M., A.P., J.R.S., K.H.E.; Investigation:

E.S.-M., D.G., J.F., E.B.-C., M.C., S.P., K.H.E.; Resources: D.G., J.R.S., K.H.E.; Data curation: E.S.-M., D.G., K.H.E.; Writing - original draft: E.S.-M., D.G., K.H.E.; Writing - review & editing: E.S.-M., D.G., J.F., A.P., E.B.-C., M.C., S.P., K.H.E.; Visualization: E.S.-M.; Supervision: D.G., K.H.E.; Project administration: D.G., J.F., K.H.E.; Funding acquisition: D.G., K.H.E., J.F.

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