CORA Cork Open Research Archive
Cartlann Taighde Oscailte Chorcaí

Title	Accelerating animal energetics: High dive costs in a small seabird disrupt the dynamic body acceleration - energy expenditure relationship
Authors	Ste Marie, Eric;Grémillet, David;Fort, Jérôme;Patterson, Allison;Brisson-Curadeau, Émile;Clairbaux, Manon;Perret, Samuel;Speakman, John;Elliott, Kyle H.
Publication date	2022-05-20
Original Citation	Ste Marie, E., Grémillet, D., Fort, J., Patterson, A., Brisson-Curadeau, É., Clairbaux, M., Perret, S., Speakman, J. and Elliott, K. H. (2022) 'Accelerating animal energetics: High dive costs in a small seabird disrupt the dynamic body acceleration - energy expenditure relationship', Journal of Experimental Biology, 225(12), jeb243252 (10pp). https://doi.org/10.1242/jeb.243252
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1242/jeb.243252
Rights	© 2022, the Authors. Published under licence by The Company of Biologists Ltd.
Download date	2026-11-15 14:05:34
Item downloaded from	https://hdl.handle.net/10468/13254



UCC
University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Accelerating animal energetics: High dive costs in a small seabird disrupt the dynamic body acceleration - energy expenditure relationship

Eric Ste Marie[1], David Grémillet[2,3], Jérôme Fort[4], Allison Patterson[1], Émile Brisson-Curadeau[1], Manon Clairbaux[5], Samuel Perret[6], John Speakman[7] and Kyle H. Elliott[1]

[1] Department of Natural Resource Sciences, McGill University, Ste Anne-de-Bellevue, Quebec, Canada
[2] Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 CNRS – La Rochelle Université, Villiers-en-Bois, France.
[3] Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa
[4] Littoral, Environnement et Sociétés (LIENSs), UMR7266 CNRS - La Rochelle Université, 17000 La Rochelle, France
[5] School of Biological, Environmental and Earth Sciences, University College Cork, Cork T23 N73K, Ireland
[6]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier
[7] Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, UK

Author contributions:
ES-M, DG, JF and KHE took part in the design and planning of the study. Data collection was undertaken by ES-M, DG, JF, EB-C, MC and SP. AP aided with the analysis of biologged acceleration data. JS processed our blood samples. All authors contributed to manuscript edits.

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 increase. 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.

© 2022. Published by The Company of Biologists Ltd.

Journal of Experimental Biology • Accepted manuscript

Average DEE for chick-rearing dovekies was 604 ± 119 kJ/d 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, diving: 9.37 X 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.

Introduction

Energy is the most important currency in animal ecology, influencing behavioural decisions, 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 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 on 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

Journal of Experimental Biology • Accepted manuscript

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 undoubtedly a revolutionary advance in the field of wildlife energetics, nearly two decades of study on a wide variety of species has revealed a few weaknesses with the use of dynamic body acceleration (DBA) as the sole predictor of metabolic rate in some animals. In a recent reappraisal of DBA's use in energetics modeling, 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 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 disproportionally affect recorded DBA without a coinciding change in energy use (Wilson et al., 2020). Therefore, DBA's relationship with energy expenditure can be variable, often requiring context- or activity-specific assessments (Elliott et al. 2013b; Elliott 2016).

For the reasons outlined above, modeling 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; Halsey et al., 2011c). 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 are 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

Journal of Experimental Biology • Accepted manuscript

vertebrates are often weak without the addition of other model parameters (Halsey, 2017; Rosen et al., 2017; Wilson et al., 2020). Several 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 and 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 modeled 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, due to 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*) 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; Harding et al., 2009b; Welcker et al., 2009). Dovekies are diving seabirds that feed on a variety of zooplankton, including fish larvae, euphausids 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 due to 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 (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.

Journal of Experimental Biology • Accepted manuscript

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 doubly labeled water (DLW) method, and individual activity profiles, derived from triaxial acceleration data. We expected dovekie dive costs to be higher than in other auk species due to 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. Since stroke frequency coincides directly with the power generated by the contraction of muscle fibres in animals that swim and/or fly (Pennycuick, 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.

Methods

Study Area & 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 doubly-labelled water (the dosage was increased in 2018 to extend the recapture window; Speakman, 1997). Of those birds, we taped small triaxial accelerometers (Axy4, Technosmart, Italy; 3.4g including tubing and tape) to the breast feathers of 60 birds to record their activity. Recaptures began approximately 20 hours after the birds were released. Body measurements (flattened wing, tarsus and beak length) were taken for each dovekie following final blood sampling.

Energy Expenditure

To estimate the average energy expenditure of each of our birds, we used the doubly labeled water (DLW) method (Speakman, 1997; Welcker et al., 2009). This method estimates carbon-dioxide production using the differential decline of heavy isotopes of hydrogen and

Journal of Experimental Biology • Accepted manuscript

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 enrichments of ^{18}oxygen and deuterium. We used the one-sample method for all our accelerometer-equipped birds to reduce handling time (handling time: ~10-15 minutes). 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 the birds not being equipped with accelerometers and whose initial isotope enrichments could be used to interpolate the initial enrichments of the one-sample birds using body mass (R^2 = 0.68-0.74 between isotopes and mass depending on year; see data appendix).

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_2O^{18}; 35% D_2O). 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 one hour 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 to 50 hours (accelerometers were removed prior to weighing). The isotopic enrichments of blood samples were measured using an isotopic water analyzer (Los Gatos, San Jose, 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 J/mL of CO_2 (Welcker et al., 2009). Daily energy expenditure (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 was assessed visually using standard residual plots (Q-Q plot and residuals vs. fitted plot).

Journal of Experimental Biology • Accepted manuscript

Accelerometry & 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 work on thick-billed murres (2019). Specifically, a fast Fourier transform, applied over a 5-second 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-second 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-second moving window of pitch was used to define periods when the dovekie was descending (pitch < -45°) or ascending (pitch >45°).

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 seconds, 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 where the bird was not ascending or descending, did not have a stroke frequency between 1 – 6 Hz, and change in pitch was less than 10° (i.e. assumed to be back at the surface). If these conditions were not met within 120 seconds (the presumed maximum dive duration), then the end of the dive was defined as 120 seconds 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 ±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 Appendix.

To estimate energetic costs in dovekies, we compared several models using activity-specific time-budgets and dynamic body acceleration as predictors. We began by conducting multiple regression analyses with activity-specific time budgets (percentages of total deployment time) as explanatory variables and mass-specific DEE as the response variable. We opted to use mass-specific DEE instead of absolute DEE to facilitate comparisons with the dynamic body acceleration models described in the next section (further justification is available in the SI appendix). Since one of the primary objectives of the study was to estimate flight and dive costs,

Journal of Experimental Biology • Accepted manuscript

three activity categories were initially selected for analysis: flying, diving and other (resting, walking, etc).

$$DEE = a(\%Time_{fly}) + b(\%Time_{dive}) + c(\%Time_{other}) \qquad \text{(Model 1)}$$

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 SI appendix). 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. Since 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 SI appendix). 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-second rolling mean to the raw acceleration data in order to remove any signal resulting from the animal's movement (e.g. wingbeats). As time's effect 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 if incorporating ODBA improved the fit of the basic time-budget model (i.e. Model 1).

Journal of Experimental Biology • Accepted manuscript

$$DEE = d(\%Time_{fly}*ODBA_{fly}) + e(\%Time_{dive}*ODBA_{dive}) + f(\%Time_{other}ODBA_{other}) \quad \text{(Model 8)}$$

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 $\Delta AIC<2$ were assumed equivalent to the best model and discussed in further detail throughout (Symonds and Moussalli, 2011). Using the coefficients resulting from selected models, we calculated predicted DEE and plotted it against doubly labeled water derived DEE. We then performed a reduced major axis (RMA) regression using the *smatr* package for R (Warton et al. 2012) to check whether predicted DEE was in close agreement with the doubly labeled water derived DEE estimates that our models were based on. To illustrate the potential relationship between DEE and ODBA (i.e. Model 7), doubly labeled water derived DEE was plotted against mean ODBA, revealing an obvious gap between points for dovekies tagged in 2017 and those tagged in 2018. Since 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 dovekies 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 sizes for each test group, residual plots (Q-Q and Residuals vs. fitted) were used to check the normality and homogeneity of variance assumptions instead of a formal test. All statistical analyses were conducted in R (R Core Team, 2018).

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 $\log_{10}$(stroke frequency) and $\log_{10}$(mass) in dovekies 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

Journal of Experimental Biology • Accepted manuscript

species was represented in both studies, we chose the value provided in Sato's paper which relied on accelerometer derived estimates instead of video analysis (Literature values presented in Supplementary Table 1). 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 to those published by Elliott et al. (2004) and Sato et al. (2007) for Alcids and marine vertebrates respectively.

Results

Due to weather and logistics constraints, 54% of the 35 deployed dovekies were recaptured in 2017 and only 31% of the 54 birds deployed in 2018. Of these, several were caught outside of the timeframe 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 DLW derived daily energy expenditure (DEE) for dovekies in 2017 and 2018 was 621 ± 103 $kJ.d^{-1}$ and 590 ± 133 $kJ.d^{-1}$, respectively (Supplementary Table 2). A two-way ANOVA showed no significant differences between estimates for both sampling years ($p=0.90$, n=11 in 2017 and n=13 in 2018), nor 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 DLW-derived DEE, 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 dovekies was 98 W kg^{-1} (95% CI= 63-133 W kg^{-1}) or approximately 7.24 X BMR (using a BMR estimate of 177.9 kJ d^{-1} for dovekies of mean mass = 152.5 g [Gabrielsen et al., 1991]). Our estimated dive cost was 126 W kg^{-1} (95% CI= 86-167 W kg^{-1}) or approximately 9.37 X BMR. Model 2, which combined time budgets for flying and diving, estimated a combined cost of 110 W kg^{-1} (95% CI=86-135 W kg^{-1}) for these behaviours (i.e. 8.16 X BMR). Figures 1A and 1B illustrate the utility of our model coefficients with regards to predicting DLW-derived DEE (RMA regression with n=13, Model 1: $R^2= 0.77$, $p=7.48x10^{-05}$, Fig.1A, and Model 2: $R^2= 0.74$, $p=0.000145$, Fig.1B). Models

Journal of Experimental Biology • Accepted manuscript

incorporating ODBA (Models 7 and 8) did not improve on time-budget models, nor did replacing percent of time spent diving with an exponential cost function (Model 6).

The tagged dovekies used in our energy expenditure modeling exhibited an overall mean ODBA of 0.41 g s^{-1} ±0.06 (SD), while activity-specific ODBA was 0.71 g s^{-1} ±0.06 for flight, 0.67 g s^{-1} ±0.07 for diving and 0.25 ±0.08 for the other behavioural category (Table 3). A one-way ANOVA showed there was significant differences in mean ODBA across behaviours ($F_{2,36}$ =167.1, p=0.000). A Tukey post-hoc test revealed that mean ODBA during flight and diving were 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 ± 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 ± 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 BMR for flight and 9.37 BMR for diving). Put together, these findings suggest that high non-mechanical costs

Journal of Experimental Biology • Accepted manuscript

such as thermoregulation during dives are weakening the relationship between ODBA and DEE (Wilson et al., 2020). Furthermore, while dive costs were relatively high compared to flight in dovekies, their average stroke frequency while diving was consistent with inter-species allometric scaling relationships. Thus, dovekies 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).

Daily Energy Expenditure

Despite rapid environmental changes in the Arctic, DEE estimates for nesting dovekies 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; 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 dovekies to buffer the effects of climate change in East Greenland (Grémillet et al. 2012). However, as prey dynamics continue to shift with increasing temperatures, dovekies 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 dovekies and these were based on allometric relationships or biomechanical modeling (i.e. the Pennycuick model; Pennycuick 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 and 11.6 X BMR (Fort et al., 2009; Gabrielsen et al., 1991). While both our

Journal of Experimental Biology • Accepted manuscript

estimated flight and dive costs fell within that range (7.24 and 9.37 X BMR), dive costs were relatively high compared to flight costs. Some species are known to trade-off time budgets for energetically costly behaviours in order to minimize overall costs (Elliott et al 2013), 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, details available in SI appendix). 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 is resulting in high energetic costs during flapping-flight. For instance, these estimates are almost double that of 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 to the flight costs of the largest auk species, the thick-billed murre (*Uria lomvia*, 31 X BMR; Elliott et al., 2013b), dovekies have relatively low flight costs. This is almost certainly because thick-billed murres have roughly two times higher wing-loading than dovekies (Gabrielsen et al. 1991; Elliott et al. 2013b), and induced flight costs increase non-linearly with wing-loading (proportionate to $(\text{Mass/wingspan})^2$; Pennycuick, 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 W kg^{-1}) with the largest (the thick-billed murre, 146 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 to other species. Though these small seabirds have short dive-adapted wings, they are still longer (relative to body size) than in other Alcids, like the thick-billed murre whose relative dive costs are typically lower than in dovekies (~40W/kg for an average length dive, Elliott et al., 2013b). Longer wings increase hydrodynamic drag when moving through the water and this translates to 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

Journal of Experimental Biology • Accepted manuscript

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 10m (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 which 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. On the other hand, as shallow divers (average depth ~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 two 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 SST for July and August = 1.70 ± 0.39 °C) than in 2017 (0.72 ± 0.47 °C), consistent with DEE in 2018 being

Journal of Experimental Biology • Accepted manuscript

lower than expected based on activity levels alone (Fig. 1; refer to the appendix for details on how bimonthly mean SSTs were 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 behaviours and energy expenditures recorded for these small birds (Sun et al., 2020).

Allometry of Stroke Frequency

Dominant stroke frequency during flight varied across individual dovekies with $Mass^{-0.42}$, 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; Pennycuick, 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 are resulting from varying fat reserves instead of overall differences in body size (Pennycuick, 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 nor 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 having lower mass-specific stroke frequencies than other swimming vertebrate taxa, the scaling exponent (-0.27) obtained for diving Alcids was

Journal of Experimental Biology • Accepted manuscript

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 being 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 dynamic body acceleration alone is not an effective predictor of daily energy expenditure 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. Since the DLW method is challenging to perform in species like dovekies, accelerometers can be used to study their energetics going forward. Additionally, the use of accelerometer-derived information in ecological modeling 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).

Journal of Experimental Biology • Accepted manuscript

Acknowledgements:

This study was funded by CNRS, the French Polar Institute Paul-Emile Victor (ADACLIM programme N°388 awarded to DG and JF), grants from the French National Research Agency (ILETOP no. ANR-16-CE34-0005 administered by P. Bustamante and ANR INTERARCTIC no. ANR-17-CE03-0009 administered by E. Gauthier), the Natural Sciences and Engineering Research Council of Canada (NSERC), and the Northern Scientific Training Program. This work is also a contribution to the project ARCTIC-STRESSOR no ANR-20-CE34-0006 awarded to JF. We are grateful for the support of NANU Travel, our logistics partner in East Greenland, as well as to the people of Ittoqqortoormiit. We also warmly thank Aurélien Prudor, Céline Albert, Anders Mosbech and Peter Lyngs for their participation in fieldwork. TechnoSmArt (Rom, Italy) provided acceleration data loggers, and we are grateful for their assistance. This is a contribution to the Excellence Chair ECOMM funded by the Region Nouvelle Aquitaine. Fieldwork was conducted under permits of the Government of Greenland - Ministry of Fishery, Hunting and Agriculture (2017-13 and 2018-2257). Parts of the results/discussion in this paper are reproduced from the PhD thesis Appendix of Manon Clairbaux (Montpellier University, 2020).

Data Sources:

While all the data pertaining to dovekies was 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).

References

Alves, J. A., Gunnarsson, T. G., Hayhow, D. B., Appleton, G. F., Potts, P. M., Sutherland, W. J. and Gill, J. A. (2013). Costs, benefits, and fitness consequences of different migratory strategies. *Ecology* **94**, 11–17.

Amélineau, F., Gremillet, D., Bonnet, D., Le Bot, T. and Fort, J. (2016). Where to forage in the absence of sea ice? Bathymetry as a key factor for an Arctic seabird. *PLoS One* **11**, e0157764.

Amélineau, F., Grémillet, D., Harding, A. M. A., Walkusz, W., Choquet, R. and Fort, J. (2019). Arctic climate change and pollution impact little auk foraging and fitness across a decade. *Sci. Rep.* **9**, 1014.

Beaugrand, G., Luczak, C. and Edwards, M. (2009). Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Chang. Biol.* **15**, 1790–1803.

Journal of Experimental Biology • Accepted manuscript

Berg, K. S., Delgado, S. and Mata-Betancourt, A. (2019). Phylogenetic and kinematic constraints on avian flight signals. *Proc. R. Soc. B* **286**, 20191083.

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., Milsom, W. K., Natsagdorj, T., Newman, S. H. and Scott, G. R. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science (80-.).* **347**, 250–254.

Burnham, K. K. and Burnham, W. A. (2005). Dovekie response to glaucous gull behavior and approach in north Greenland. *Dan Ornitol Foren Tidsskr* **99**, 115–118.

Butler, P. J. (2006). Aerobic dive limit. What is it and is it always used appropriately? *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **145**, 1–6.

Butler, P. J., Green, J. A., Boyd, I. L. and Speakman, J. R. (2004). Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Funct. Ecol.* **18**, 168–183.

Cavagna, G. A., Saibene, F. P. and Margaria, R. (1963). External work in walking. *J. Appl. Physiol.* **18**, 1–9.

Clairbaux, M., Fort, J., Mathewson, P., Porter, W., Strøm, H. and Grémillet, D. (2019). Climate change could overturn bird migration: Transarctic flights and high-latitude residency in a sea ice free Arctic. *Sci. Rep.* **9**, 1–13.

Croll, D. A. and McLaren, E. (1993). Diving metabolism and thermoregulation in common and thick-billed murres. *J. Comp. Physiol. B* **163**, 160–166.

Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P. and Green, J. A. (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Sci. Rep.* **10**, 1–11.

Elliott, K. H. (2016). Measurement of flying and diving metabolic rate in wild animals: review and recommendations. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **202**, 63–77.

Elliott, K. H. and Gaston, A. J. (2014). Dive behaviour and daily energy expenditure in thick-billed Murres Uria lomvia after leaving the breeding colony. *Mar. Ornithol.* **42**, 183–189.

Elliott, K. H., Hewett, M., Kaiser, G. W. and Blake, R. W. (2004). Flight energetics of the Marbled Murrelet, Brachyramphus marmoratus. *Can. J. Zool.* **82**, 644–652.

Elliott, K. H., Davoren, G. K. and Gaston, A. J. (2007). The influence of buoyancy and drag on the dive behaviour of an Arctic seabird, the Thick-billed Murre. *Can. J. Zool.* **85**, 352–361.

Elliott, K. H., Le Vaillant, M., Kato, A., Speakman, J. R. and Ropert-Coudert, Y. (2013a). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biol. Lett.* **9**, 20120919.

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R. and Davoren, G. K. (2013b). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci.* **110**, 9380–9384.

Journal of Experimental Biology • Accepted manuscript

Elliott, K. H., Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., Osborne, O., Ropert-Coudert, Y., Speakman, J. R. and Hare, J. F. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Mov. Ecol.* **2**, 1–15.

Flint, E. N. and Nagy, K. A. (1984). Flight energetics of free-living sooty terns. *Auk* **101**, 288–294.

Fort, J., Porter, W. P. and Grémillet, D. (2009). Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *J. Exp. Biol.* **212**, 2483–2490.

Fort, J., Cherel, Y., Harding, A. M. A., Egevang, C., Steen, H., Kuntz, G., Porter, W. P. and Grémillet, D. (2010). The feeding ecology of little auks raises questions about winter zooplankton stocks in North Atlantic surface waters. *Biol. Lett.* **6**, 682–684.

Fort, J., Porter, W. P. and Grémillet, D. (2011). Energetic modelling: a comparison of the different approaches used in seabirds. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **158**, 358–365.

Fox, J. and Weisberg, S. (2019). An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M. and Mehlum, F. (1991). Field and laboratory metabolism and thermoregulation in dovekies (Alle alle). *Auk* **108**, 71–78.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L. and Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends Ecol. Evol.* **26**, 285–291.

González-Bergonzoni, I., Johansen, K. L., Mosbech, A., Landkildehus, F., Jeppesen, E. and Davidson, T. A. (2017). Small birds, big effects: the little auk (Alle alle) transforms high Arctic ecosystems. *Proc. R. Soc. B Biol. Sci.* **284**, 20162572.

Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and recommendations. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **158**, 287–304.

Grémillet, D., Welcker, J., Karnovsky, N. J., Walkusz, W., Hall, M. E., Fort, J., Brown, Z. W., Speakman, J. R. and Harding, A. M. A. (2012). Little auks buffer the impact of current Arctic climate change. *Mar. Ecol. Prog. Ser.* **454**, 197–206.

Grémillet, D., Lescroël, A., Ballard, G., Dugger, K. M., Massaro, M., Porzig, E. L. and Ainley, D. G. (2018). Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Funct. Ecol.* **32**, 1203–1213.

Halsey, L. G. (2017). Relationships grow with time: a note of caution about energy expenditure-proxy correlations, focussing on accelerometry as an example. *Funct. Ecol.* **31**, 1176–1183.

Halsey, L. G., Shepard, E. L. C. and Wilson, R. P. (2011a). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **158**, 305–314.

Halsey, L. G., White, C. R., Enstipp, M. R., Wilson, R. P., Butler, P. J., Martin, G. R., Grémillet, D. and Jones, D. R. (2011b). 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.

Journal of Experimental Biology • Accepted manuscript

Halsey, L. G., Jones, T. T., Jones, D. R., Liebsch, N. and Booth, D. T. (2011c). Measuring energy expenditure in sub-adult and hatchling sea turtles via accelerometry. *PLoS One* **6**, e22311.

Harding, A. M. A., Egevang, C., Walkusz, W., Merkel, F., Blanc, S. and Grémillet, D. (2009a). Estimating prey capture rates of a planktivorous seabird, the little auk (Alle alle), using diet, diving behaviour, and energy consumption. *Polar Biol.* **32**, 785–796.

Harding, A. M. A., Kitaysky, A. S., Hall, M. E., Welcker, J., Karnovsky, N. J., Talbot, S. L., Hamer, K. C. and Grémillet, D. (2009b). Flexibility in the parental effort of an Arctic-breeding seabird. *Funct. Ecol.* **23**, 348–358.

Hicks, O., Burthe, S., Daunt, F., Butler, A., Bishop, C. and Green, J. A. (2017). Validating accelerometry estimates of energy expenditure across behaviours using heart rate data in a free-living seabird. *J. Exp. Biol.* **220**, 1875–1881.

Hicks, O., Kato, A., Angelier, F., Wisniewska, D. M., Hambly, C., Speakman, J. R., Marciau, C. and Ropert-Coudert, Y. (2020). Acceleration predicts energy expenditure in a fat, flightless, diving bird. *Sci. Rep.* **10**, 21493.

Kidawa, D., Jakubas, D., Wojczulanis-Jakubas, K., Stempniewicz, L., Trudnowska, E., Boehnke, R., Keslinka-Nawrot, L. and Błachowiak-Samołyk, K. (2015). Parental efforts of an Arctic seabird, the little auk Alle alle, under variable foraging conditions. *Mar. Biol. Res.* **11**, 349–360.

Lear, K. O., Whitney, N. M., Brewster, L. R., Morris, J. J., Hueter, R. E. and Gleiss, A. C. (2017). Correlations of metabolic rate and body acceleration in three species of coastal sharks under contrasting temperature regimes. *J. Exp. Biol.* **220**, 397–407.

Lovvorn, J. R. (2007). Thermal substitution and aerobic efficiency: measuring and predicting effects of heat balance on endotherm diving energetics. *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 2079–2093.

Lovvorn, J. R. and Jones, D. R. (1991). Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (Aythya spp.). *Can. J. Zool.* **69**, 2879–2887.

Lovvorn, J. R., Watanuki, Y., Kato, A., Naito, Y. and Liggins, G. A. (2004). Stroke patterns and regulation of swim speed and energy cost in free-ranging Brunnich's guillemots. *J. Exp. Biol.* **207**, 4679–4695.

Meir, J. U., Stockard, T. K., Williams, C. L., Ponganis, K. V and Ponganis, P. J. (2008). Heart rate regulation and extreme bradycardia in diving emperor penguins. *J. Exp. Biol.* **211**, 1169–1179.

Murchie, K. J., Cooke, S. J., Danylchuk, A. J. and Suski, C. D. (2011). Estimates of field activity and metabolic rates of bonefish (Albula vulpes) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. *J. Exp. Mar. Bio. Ecol.* **396**, 147–155.

Niizuma, Y., Gabrielsen, G. W., Sato, K., Watanuki, Y. and Naito, Y. (2007). Brünnich's guillemots (Uria lomvia) maintain high temperature in the body core during dives. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **147**, 438–444.

Journal of Experimental Biology • Accepted manuscript

Patterson, A., Gilchrist, H. G., Chivers, L., Hatch, S. and Elliott, K. (2019). A comparison of techniques for classifying behavior from accelerometers for two species of seabird. *Ecol. Evol.* **9**, 3030–3045.

Pennycuick, C. J. (1989). *Bird flight performance*. Oxford University Press.

Pennycuick, C. J. (2008). *Modelling the flying bird*. Elsevier.

R Core Team (2018). R: A Language and Environment for Statistical Computing.

Richman, S. E. and Lovvorn, J. R. (2011). Effects of air and water temperatures on resting metabolism of auklets and other diving birds. *Physiol. Biochem. Zool.* **84**, 316–332.

Rosen, D. A. S., Hindle, A. G., Gerlinsky, C. D., Goundie, E., Hastie, G. D., Volpov, B. L. and Trites, A. W. (2017). Physiological constraints and energetic costs of diving behaviour in marine mammals: a review of studies using trained Steller sea lions diving in the open ocean. *J. Comp. Physiol. B* **187**, 29–50.

Sato, K., Watanuki, Y., Takahashi, A., Miller, P. J. O., Tanaka, H., Kawabe, R., Ponganis, P. J., Handrich, Y., Akamatsu, T. and Watanabe, Y. (2007). Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. B Biol. Sci.* **274**, 471–477.

Schultner, J., Welcker, J., Speakman, J. R., Nordøy, E. S. and Gabrielsen, G. W. (2010). Application of the two-sample doubly labelled water method alters behaviour and affects estimates of energy expenditure in black-legged kittiwakes. *J. Exp. Biol.* **213**, 2958–2966.

Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. (2013). Energy landscapes shape animal movement ecology. *Am. Nat.* **182**, 298–312.

Speakman, J. (1997). *Doubly labelled water: theory and practice*. Springer Science & Business Media.

Stothart, M. R., Elliott, K. H., Wood, T., Hatch, S. A. and Speakman, J. R. (2016). Counting calories in cormorants: dynamic body acceleration predicts daily energy expenditure measured in pelagic cormorants. *J. Exp. Biol.* **219**, 2192–2200.

Sun, A., Whelan, S., Hatch, S. A. and Elliott, K. H. (2020). Tags below three percent of body mass increase nest abandonment by rhinoceros auklets, but handling impacts decline as breeding progresses. *Mar. Ecol. Prog. Ser.* **643**, 173–181.

Sutton, G. J., Botha, J. A., Speakman, J. R. and Arnould, J. P. Y. (2021). Validating accelerometry-derived proxies of energy expenditure using the doubly labelled water method in the smallest penguin species. *Biol. Open* **10**, bio055475.

Symonds, M. R. E. and Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65**, 13–21.

Taylor, J. R. E. (1994). Changes in body mass and body reserves of breeding Little Auks (Alle alle L.). *Polish Polar Res.* 147–168.

Videler, J. J. (2006). *Avian flight*. Oxford University Press.

Warton, D. I., Duursma, R. A., Falster, D. S. and Taskinen, S. (2012) smatr 3 - an R package for estimation and inference about allometric lines *Methods in Ecology and Evolution*, **3**(2), 257-259.

Journal of Experimental Biology • Accepted manuscript

Welcker, J., Harding, A. M. A., Kitaysky, A. S., Speakman, J. R. and Gabrielsen, G. W. (2009). Daily energy expenditure increases in response to low nutritional stress in an Arctic- breeding seabird with no effect on mortality. *Funct. Ecol.* **23**, 1081–1090.

Wilson, R. P., Hustler, K., Ryan, P. G., Burger, A. E. and Noldeke, E. C. (1992). Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Am. Nat.* **140**, 179–200.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (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.

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez- Laich, A., Quintana, F., Rosell, F., Graf, P. M., Williams, H. and Gunner, R. (2020). Estimates for energy expenditure in free- living animals using acceleration proxies: A reappraisal. *J. Anim. Ecol.* **89**, 161–172.

Journal of Experimental Biology • Accepted manuscript

Figures and Tables

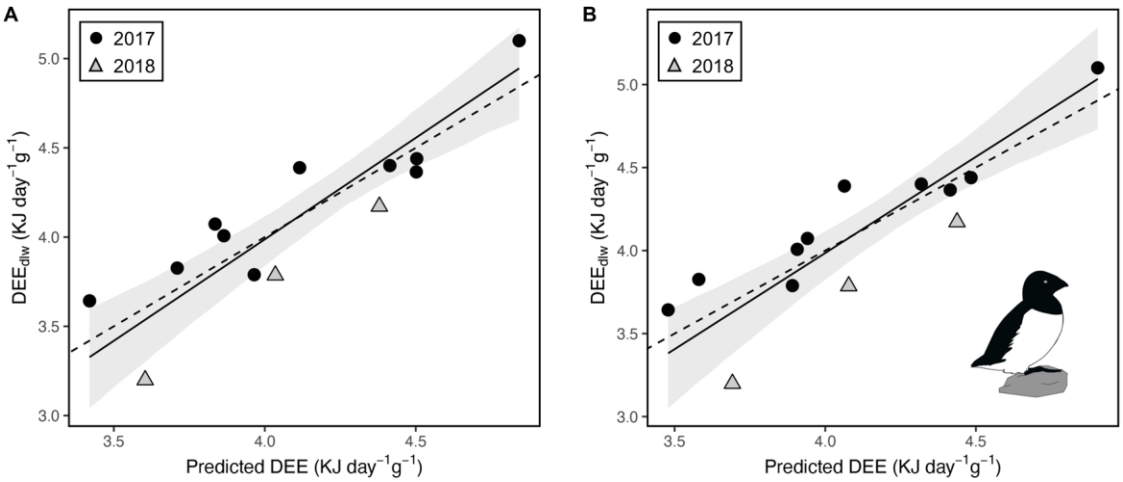


Figure 1: Time-budget predicted daily energy expenditure for the two model variants with ΔAIC<2 (Model 1 [A] and Model 2 [B]) plotted against doubly labeled water derived estimates of daily energy expenditure (DEE_{dlw}). Black lines represent the output of a reduced major axis regression with shaded regions depicting 95% confidence intervals (n=13, Model 1: R^2= 0.77, p<0.0001, DEE_{dlw} = 1.14(Predicted DEE) – 0.56; Model 2: R^2= 0.74, p<0.001, DEE_{dlw} = 1.16(Predicted DEE) – 0.65;). Dashed lines depict the lines of equality (i.e. 1:1 relationship).

Journal of Experimental Biology • Accepted manuscript

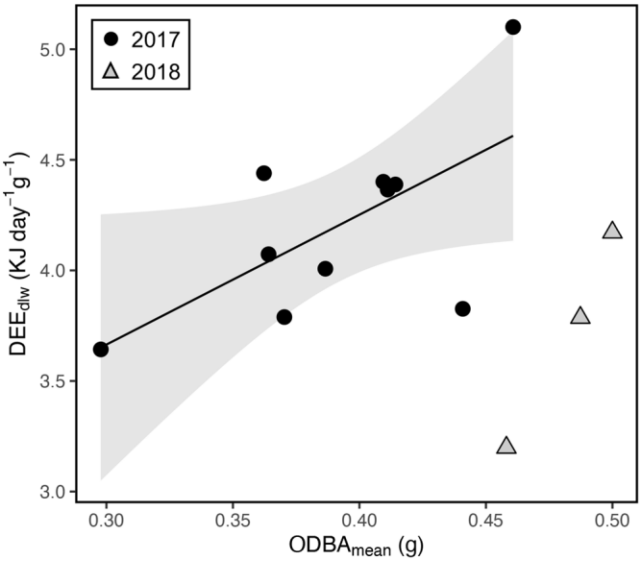


Figure 2: Doubly labeled water derived estimates of daily energy expenditure (DEE_{dlw}) plotted against time-averaged overall dynamic body acceleration ($ODBA_{mean}$). There was a weak significant linear relationship between DEE_{dlw} and $ODBA_{mean}$ for dovekies tagged in 2017 (R^2=0.41, p<0.05, n=10; DEE_{dlw}= 5.87($ODBA_{mean}$)+ 1.90; shaded region represents the 95% confidence intervals), but none for the combined datasets of 2017 and 2018 (p>0.05, n=13).

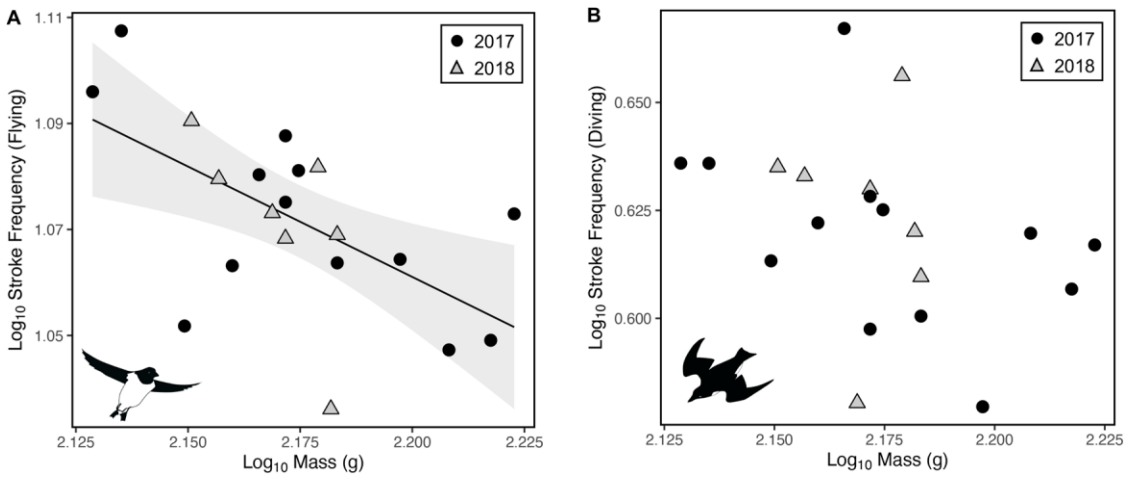


Figure 3: Dominant stroke frequencies (Hz) plotted against mass for (A) flying (Stoke frequency = 94.914[Mass]$^{-0.416}$; p< 0.01, R^2= 0.35, n=20) and (B) diving dovekies (no significant relationship).

Journal of Experimental Biology • Accepted manuscript

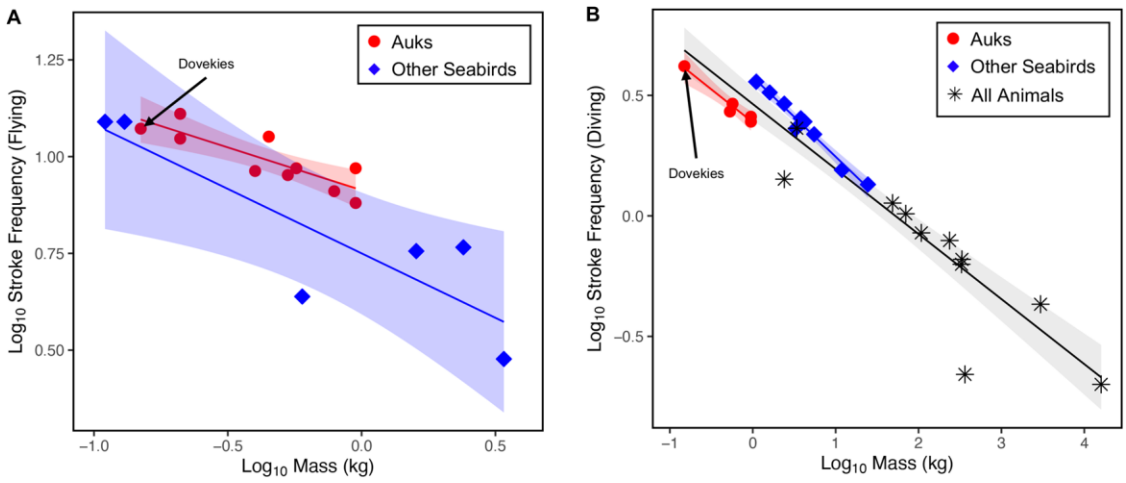


Figure 4: Mean stroke frequencies (Hz) plotted against mass for (A) flying and (B) diving animals. In panel (B), the "All animals" trendline is inclusive of "Auks" and "Other Seabirds". All data points aside from those for dovekies are derived from previous research by Sato et al. (2007) and Elliott et al. (2004). Stroke frequency varied significantly with mass across auks during flight (Stoke 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 dovekies are indicated by black arrows.

Table 1: ΔAIC comparison of time budget (n=6) and ODBA (n=2) models used to explain doubly-labeled water estimates of mass-specific daily energy expenditure in dovekies equipped with accelerometers (n=13). Akaike weights are presented alongside delta AIC.

ID	Model	ΔAIC	Weights
2	$\%\text{Time}_{\text{fly+dive}} + \%\text{Time}_{\text{other}}$	0.00	0.48
1	$\%\ \text{Time}_{\text{fly}} + \%\ \text{Time}_{\text{dive}} + \%\text{Time}_{\text{other}}$	0.47	0.38
5	$\%\ \text{Time}_{\text{fly}} + \%\ \text{Time}_{\text{dive}} + \%\text{Time}_{\text{rest}} + \%\text{Time}_{\text{unknown}}$	2.36	0.15
3	$\%\ \text{Time}_{\text{dive}} + \%\text{Time}_{\text{other+fly}}$	12.51	0.00
6	$\%\ \text{Time}_{\text{fly}} + \sum(1\text{-}e^{\text{-duration}/19.68}) + \%\text{Time}_{\text{other}}$	12.98	0.00
8	$\%\text{Time}_{\text{fly}}*\text{ODBA}_{\text{fly}} + \%\text{Time}_{\text{dive}}*\text{ODBA}_{\text{dive}} + \%\text{Time}_{\text{other}}*\text{ODBA}_{\text{other}}$	13.54	0.00
4	$\%\ \text{Time}_{\text{fly}} + \%\text{Time}_{\text{other+dive}}$	14.70	0.00
7	$\text{ODBA}_{\text{mean}}$	17.62	0.00

Journal of Experimental Biology • Accepted manuscript

Table 2: Output of the best models (ΔAIC<2) for explaining doubly-labeled water estimates of mass-specific daily energy expenditure in dovekies equipped with accelerometers. 95% confidence intervals are presented in brackets beside each estimate.

	Activity cost		
	***kJ $d^{-1}g^{-1}$**	**W kg^{-1}**	****BMR**
$\%Time_{fly+dive}$	9.52 (7.40-11.63)	110.1 (85.7-134.6)	8.16 (6.35-9.97)
$\%Time_{other}$	0.97 ([-0.25]-2.19)	11.2 ([-2.9]-25.4)	0.83 ([-0.21]-1.88)
$\%Time_{fly}$	8.45 (5.44-11.45)	97.8 (63.0-132.5)	7.24 (4.67-9.82)
$\%Time_{dive}$	10.93 (7.41-14.45)	126.5 (85.7-167.2)	9.37 (6.35-12.38)
$\%Time_{other}$	0.86 ([-0.38]-2.10)	10.0 ([-4.4]-24.3)	0.74 ([-0.33]-1.80)

*Since 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 $d^{-1}g^{-1}$).
**Activity cost estimates presented as multiples of basal metabolic rate (BMR) using a previously published value (BMR = 177.9 KJ d^{-1}, n=16, at mean body mass = 152.5 g; Gabrielsen et al. 1991).

Table 3: Overall mean and activity-specific time-averaged ODBA for the accelerometer tagged dovekies used in our daily energy expenditure modeling. Standard deviations (SD) are provided beside estimates.

	Time averaged ODBA (g s^{-1})								
Year	**Mean**	**±SD**	**Flying**	**±SD**	**Diving**	**±SD**	**Other**	**±SD**	**n**
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**

Journal of Experimental Biology • Accepted manuscript

Supporting Information

Mass specific DEE in Modeling

Given the complex relationship between mass and dynamic body acceleration (Wilson et al. 2021), we opted to use mass-specific DEE in all our modeling (i.e. ignoring potential non-linear effects of mass on DEE). To check our assumption that mass-specific DEE was a reasonable response variable to use in our energetics modeling, we conducted the following supplementary analysis. We performed a generalized linear model analysis with absolute DEE as the response variable and body mass, percent time flying, and percent time diving as explanatory variables. We then calculated the partial residuals for mass by subtracting the energy expenditure estimated using the coefficients for percent time flying (a) and diving (b) from the doubly labeled water estimate of absolute DEE. Using those partial residuals, we calculated the expected DEE for each bird assuming average time budgets for flying (17.9%) and diving (18.6%).

$$DEE_{expected} = \text{partial residuals} + a(17.9) + b(18.6)$$

Following this, we conducted a linear regression analysis between $\log_{10}(DEE_{expected})$ and $\log_{10}(\text{Body mass})$. This yielded a slope (scaling exponent) of 1.027 (CI 95% =0.31-1.74; SI Figure 2). Since mass-specific DEE assumes an allometric scaling exponent of 1, this result provides some support for our decision to use mass-specific DEE in our modeling instead of absolute DEE.

Model Variants

<u>Model variants 2-4:</u>

These variants use different combinations of the basic time-budget categories from Model 1. All time budget percentages in each model add up to 100%.

(2) $DEE \sim \%\ Time_{fly+dive} + \%Time_{other}$
(3) $DEE \sim \%\ Time_{dive} + \%Time_{other+fly}$
(4) $DEE \sim \%\ Time_{fly} + \%Time_{other+dive}$

<u>Model variant 5:</u>

$$DEE \sim \%\ Time_{fly} + \%\ Time_{dive} + \%Time_{rest} + \%Time_{unknown}$$

This variant split the “other” (i.e. not diving or flying) time budget into “resting on land” and “unknown”. Dovekies were assumed to be resting on land when their 60-second smoothed ODBA was approximately zero. This was decided after visual inspection of ODBA through time for several birds which appeared to show little to no activity for extended periods. We named

Journal of Experimental Biology • Supplementary information

this category "resting on land" instead of just "resting" since wave action would likely lead to higher ODBA values when resting on water.

Model variant 6:

$$DEE \sim \%\ Time_{fly} + \sum (1\text{-}e^{-duration/19.68}) + \%Time_{other}$$

The exponential model for diving dovekies is based on measurements of partial pressure of oxygen in emperor penguins, the only equivalent measurements in a bird that we are aware of, and where oxygen levels declined exponentially with dive duration (Ponganis et al. 2007). An exponential model during diving also improved fit with daily energy expenditure in thick-billed murres (Elliott et al. 2013). The coefficient (19.68) is derived from the coefficient for murres ($73.8\ s^{-1}$) corrected (divided by 3.75) for the ratio in average maximum dive duration between murres in that study and dovekies in our study.

Time budget trade-off

We tested for a Pearson correlation between time budgets for flight and diving (i.e. % of total deployment time) across all accelerometer tagged dovekies (n=20). We found that the time budgets were negatively correlated (R= -0.61, SI Figure 3).

Local Sea Surface Temperatures

We estimated mean local sea surface temperatures (SST) for July and August in both 2017 and 2018 in a 160 X 200 km plot surrounding the dovekie breeding colony, which previous GPS work has shown includes their foraging range (as per the methods detailed in Amélineau et al. 2019). Monthly SST data was downloaded from the Multi-scale Ultra-high Resolution (MUR) SST Analysis Anomaly (version 4.1, global 0.01° resolution) available through the National Oceanic and Atmospheric Association (NOAA).

References

Amélineau, F. *et al.* Arctic climate change and pollution impact little auk foraging and fitness across a decade. *Sci. Rep.* **9**, 1014 (2019).

Elliott, K.H., Ricklefs, R.E., Gaston, A.J., Hatch, S.A., Speakman, J.R., Davoren, G.K. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. Proc Natl Acad Sci. **110**(23):9380–9384 (2013)

Journal of Experimental Biology • Supplementary information

Ponganis, P. J. et al. Returning on empty: extreme blood O2 depletion underlies dive capacity of emperor penguins. J. Exp. Biol. **210**, 4279–4285 (2007).

Wilson, R.P. et al. Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. J Anim Ecol. **89**(1):161–172. (2020)

Journal of Experimental Biology • Supplementary information

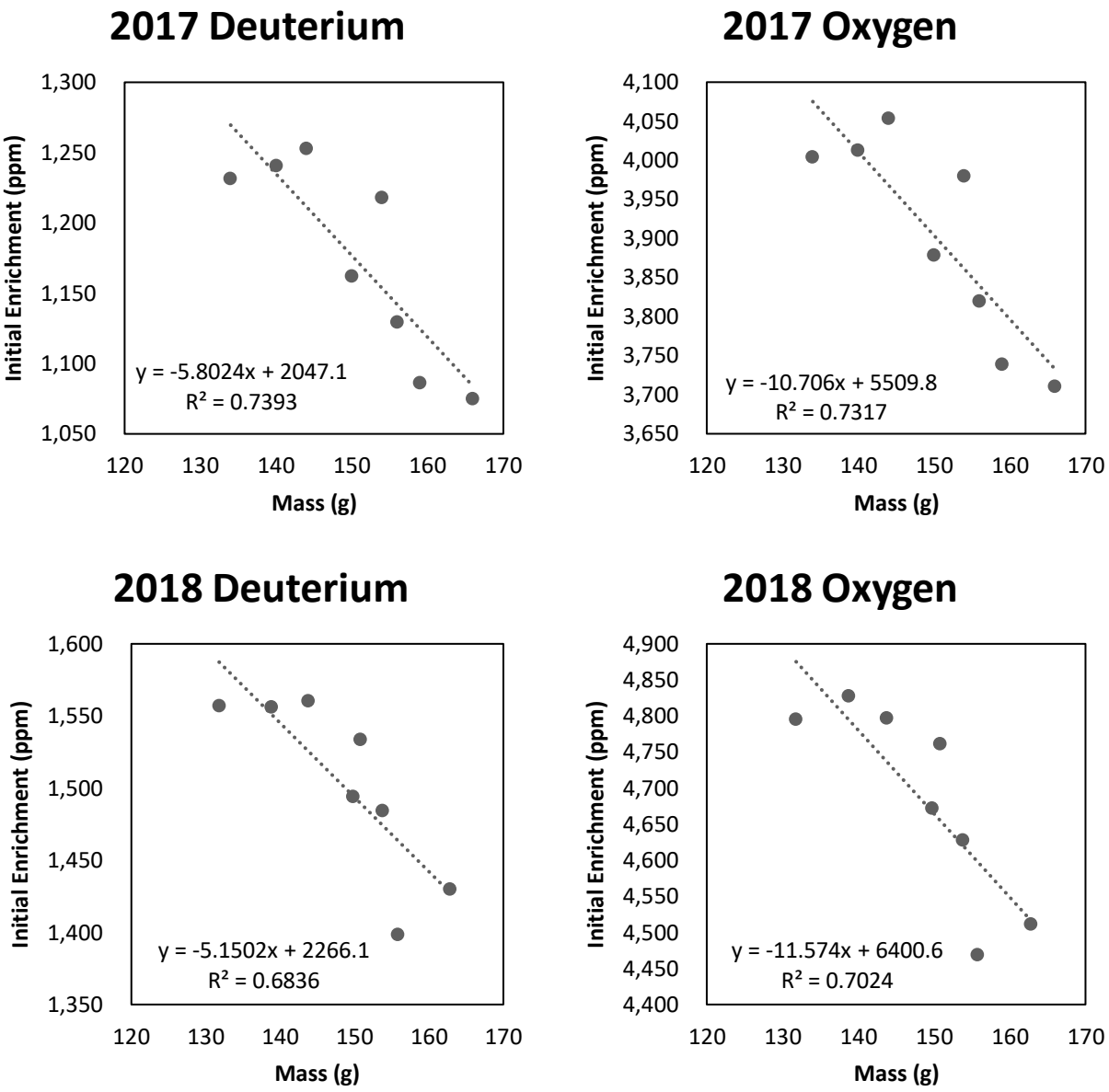


Fig. S1. Initial enrichments of deuterium and ^{18}oxygen as a function of body mass for all two-sample birds injected with DLW. Initial blood samples were taken one hour post-injection.

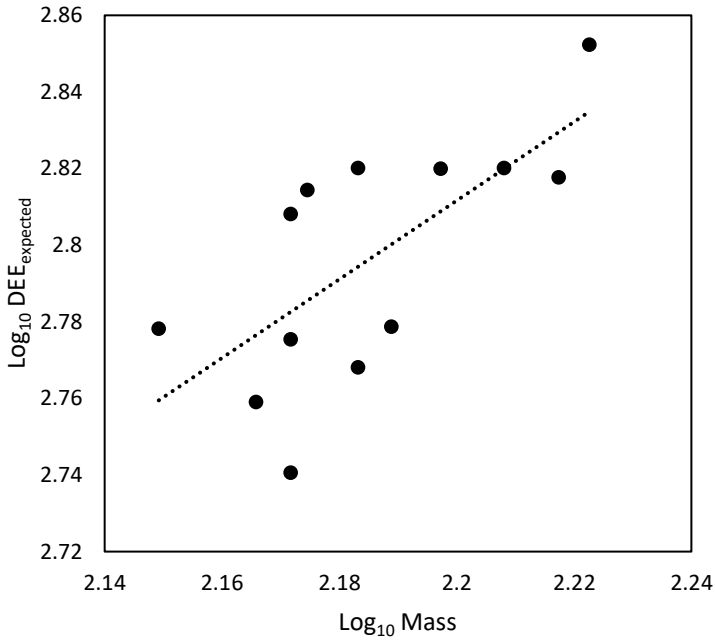


Fig. S2. Plot depicting the relationship between $DEE_{expected}$ and body mass (R^2=0.48, n=13).

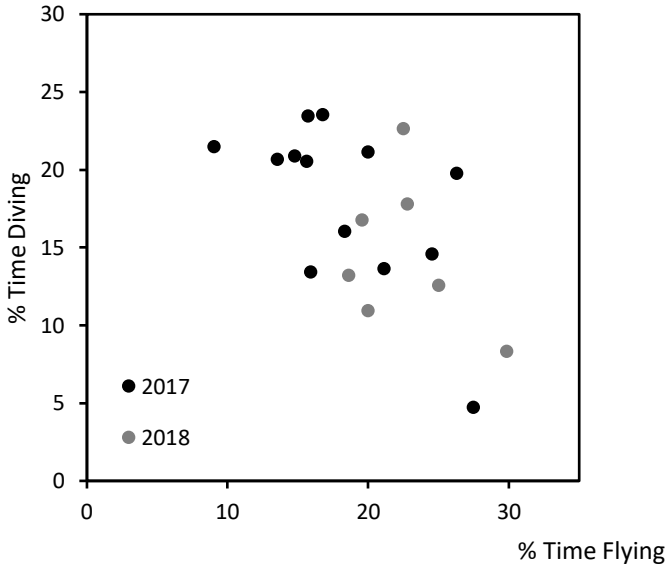


Fig. S3. Comparison of the time budgets (% of total deployment duration) for flight and diving across accelerometer-equipped dovekies (n=20).

Journal of Experimental Biology • Supplementary information

Table S1. Literature derived dominant stroke frequencies for diving and flying marine animals.

Reference	Group	Species	Mass (kg)	Stroke Frequency (Hz)				N
				Flying	±SD	Swimming	±SD	
Sato et al. 2007	Auk	Alca torda	0.57	9.33		2.92		3
Elliott et al. 2004	Auk	Alca torda	0.62	9.80	0.58			22
Present study	Auk	Alle alle	0.15	11.81	0.47	4.18	0.21	20
Elliott et al. 2004	Auk	Brachyramphus marmoratus	0.21	12.90	2.00			25
Elliott et al. 2004	Auk	Cepphus columba	0.45	11.26	1.56			4
Sato et al. 2007	Auk	Cerorhincha monocerata	0.53	8.96		2.71		3
Elliott et al. 2004	Auk	Cerorhincha monocerata	0.45	10.12	1.47			21
Elliott et al. 2004	Auk	Fratercula arctica	0.4	9.18	0.48			14
Elliott et al. 2004	Auk	Fratercula cirrhata	0.79	8.14	0.65			13
Elliott et al. 2004	Auk	Synthliboramphus antiquus	0.21	11.13	1.68			10
Sato et al. 2007	Auk	Uria aalge	0.95	9.33		2.58		3
Elliott et al. 2004	Auk	Uria aalge	0.95	8.69	0.48			61
Sato et al. 2007	Auk	Uria lomvia	0.95	7.59		2.46		3
Sato et al. 2007	Fish	Oncorhynchus keta	3.4			2.31		2
Sato et al. 2007	Fish	Paralichthys olivaceus	2.4			1.42		5
Sato et al. 2007	Mammal	Leptonychotes weddellii (adult)	330			0.63		15
Sato et al. 2007	Mammal	Leptonychotes weddellii (pup)	108			0.85		8
Sato et al. 2007	Mammal	Mirounga angustirostris	333.5			0.66		2
Sato et al. 2007	Mammal	Mirounga leonina	236.7			0.79		3
Sato et al. 2007	Mammal	Neophocaena phocaenoides	48.6			1.13		2
Sato et al. 2007	Mammal	Orcinus orca	2962			0.43		9
Sato et al. 2007	Mammal	Phoca sibirica	70.1			1.02		3
Sato et al. 2007	Mammal	Physeter macrocephalus	15951			0.20		11
Sato et al. 2007	Other Seabird	Aptenodytes forsteri	24.5			1.35		7
Sato et al. 2007	Other Seabird	Aptenodytes patagonicus	11.9			1.55		5
Sato et al. 2007	Other Seabird	Calonectris leucomelas	0.6	4.35				5
Sato et al. 2007	Other Seabird	Diomedea melanophris	3.4	3.00				4
Sato et al. 2007	Other Seabird	Eudyptes chrysolophus	3.3			2.30		8
Sato et al. 2007	Other Seabird	Eudyptula minor	1.1			3.60		5

Journal of Experimental Biology • Supplementary information

Elliott et al. 2004	Other Seabird	Pelecanoides georgicus	0.11	12.30	0.64		13
Elliott et al. 2004	Other Seabird	Pelecanoides urinatrix	0.13	12.30	0.64		14
Sato et al. 2007	Other Seabird	Phalacrocorax aristotelis	1.6	5.70		3.25	5
Sato et al. 2007	Other Seabird	Phalacrocorax georgianus	2.4	5.83		2.92	6
Sato et al. 2007	Other Seabird	Pygoscelis adeliae	4.2			2.46	17
Sato et al. 2007	Other Seabird	Pygoscelis antarctica	3.8			2.54	7
Sato et al. 2007	Other Seabird	Pygoscelis papua	5.5			2.18	5
Sato et al. 2007	Turtle	Dermochelys coriacea	363			0.22	9

Journal of Experimental Biology • Supplementary information

Table S2. Summary of daily energy expenditures (DEE) for nesting dovekies studied in Ukaleqarteq, East Greenland (70° 43' N, 21° 33 W) in 2017 and 2018.

Year	Bird	Protocol	Mass[a] (g)	Deployment Duration (hours)	KJ day^{-1}	KJ day^{-1}g^{-1}
2017	1	1-sample	157.5	21.6	602.6	3.83
2017	2	1-sample	165.0	35.5	720.3	4.37
2017	3	1-sample	152.5	23.4	621.1	4.07
2017	4	1-sample	167.0	24.2	608.3	3.64
2017	5	1-sample	148.5	27.8	659.2	4.44
2017	6	1-sample	141.0	22.3	565.1	4.01
2017	7	1-sample	149.5	21.9	656.1	4.39
2017	8	1-sample	146.5	19.8	555.1	3.79
2017	9	1-sample	148.5	36.5	757.4	5.10
2017	10	1-sample	161.5	27.4	710.7	4.40
2017	11	2-sample	148.0	21.0	379	2.56
2017	**Mean**		**153.2**	**25.6**	**621.4**	**4.05**
2018	12	1-sample	152.5	32.1	577.4	3.79
2018	13[b]	1-sample	134.5	27.2	655.7	4.88
2018	14	1-sample	148.5	35.2	475.0	3.20
2018	15	1-sample	154.5	20.3	644.5	4.17
2018	16	2-sample	154.0	52.6	538.4	3.50
2018	17	2-sample	140.0	30.5	512.4	3.66
2018	18	2-sample	159.5	31.5	567.5	3.56
2018	19	2-sample	159.5	30.3	542.1	3.40
2018	20	2-sample	148.5	19.7	560.7	3.78
2018	21	2-sample	144.5	49.5	579.6	4.01
2018	22	2-sample	152.5	23.1	992.2	6.51
2018	23	2-sample	152.0	35.4	460.4	3.03
2018	24	2-sample	132.0	43.8	565.8	4.29
2018	**Mean**		**148.7**	**33.2**	**590.1**	**4.00**

[a]The value reported here represents the average of initial mass and post-deployment mass.
[b]Accelerometer stopped recording during deployment.

Journal of Experimental Biology • Supplementary information

Supplementary Code

Automatic Dive Classification R-Code

```
#Functions
diveDefinition <- function(accdata, diveIDX, maxDive, frequency, minWBF, maxWBF,
changePitch, meanPitch) {
  theDives <- rep(NA, nrow(accdata))
  for (dive in 1:length(diveIDX)) {
    #dive <- dive + 1
    diveStart <- diveStarts[dive]
    diveEnd <- diveStart + (maxDive * frequency)
    myDive <- accdata[accdata$FID %in% diveStart:diveEnd,]
    myDive$Angle[which(myDive$Angle == "Unknown" & myDive$WBF > minWBF &
myDive$WBF < maxWBF)] <- "Stroke"
    myDive$Angle[which(myDive$Angle == "Unknown" & abs(myDive$dPitch) >
changePitch)] <- "Pitchy"
    myDive$Angle <- filterClass(myDive$Angle, 2)
    downTime <- length(myDive$Angle[myDive$Session == myDive$Session[1]])

    if (is.na(myDive$AccDive[1]) & max(myDive$pitch > 0)) {

      k <- downTime
      while ((myDive$Angle[k] == "Down") & (k < (maxDive - 1))) k <- k + 1
      while ((mean(myDive$pitch[1:k]) < meanPitch) & (k < (maxDive - 1))) k <- k + 1
      while ((!(myDive$Angle[k] %in% c("Unknown", "Flying")) & (k < (maxDive - 1)))) k <- k
+ 1

      diveEnd <- k
      diveEnd <- myDive$FID[diveEnd]
      theDives[accdata$FID %in% diveStart:diveEnd] <- dive

      plotdat <- melt(myDive[,c("FID", "pitch","dPitch","WBF","WBF3","Angle")], id =
c("FID","Angle"))
      names(plotdat) <- c("Time", "Angle","Data", "Value")
      head(plotdat)

      ggplot(plotdat, aes(Time, Value)) +
        geom_hline(yintercept = 0, col = "red") +
        geom_line() +
        geom_point(aes(col = Angle)) +
        facet_grid(Data ~ ., scales= "free_y") +
        geom_vline(xintercept = diveEnd, linetype = 3)

    }
  }
```

Journal of Experimental Biology • Supplementary information

```
  return(theDives)
}

filterClass <- function(rawClassification, mintime) {
  output <- rawClassification
  for (i in 2:(length(output) - mintime)) {
    temp <- output[i:(i + (mintime - 1))]
    temp <- ifelse(temp == "Diving", "Swimming", temp)
    tt <- which(names(table(temp)) == temp[1])
    if (table(temp)[tt] != mintime) output[i] <- output[i - 1]
  }
  output
}

getSessions <- function(behaviour, maxSession) {
  output <- 1
  j <- 1
  k <- 0
  for (i in 2:length(behaviour)) {
    j <- ifelse(behaviour[i] == behaviour[i - 1], j, j + 1)
    k <- ifelse(behaviour[i] == behaviour[i - 1], k + 1, 0)
    if (k >= maxSession) {
      j <- j + 1
      k <- 0
    }
    output[i] <- j
  }
  output
}

#############
library(caret)
library(zoo)
library(ggplot2)
library(doBy)
library(reshape2)

options(scipen = 4)
setwd("File location")
fileNames <- list.files()
fileNames

# Create thresholds for dive classification, you might want to try tweaking these to improve the
classification
downPitch <- -45
upPitch <- 45
```

Journal of Experimental Biology • Supplementary information

```
flight <- 10
startminWBF <- 1
startmaxWBF <- 6
maxTime <- 120
freq <- 50
pitchChange <- 10
pitchMean <- -20

##########################################
myData <- read.csv(file.choose(), header = T)
myData$time <- as.POSIXct(strptime(as.character(myData$time), "%Y-%m-%d
%H:%M:%OS"))

head(myData)

# Calculate some new statistics for the classification: change in pitch, mean pitch, mean WBF
myData$dPitch <- c(NA,myData$pitch[2:nrow(myData)] - myData$pitch[1:(nrow(myData) -
1)])
myData$Pitch3 <- rollapply(myData$pitch, 3, sum, fill = NA, align = "right")
myData$WBF3 <- rollapply(myData$WBF, 3, mean, fill = NA, align = "left")

# Calculate angles
myData$Angle <- "Unknown"
myData$Angle[myData$Pitch3 < downPitch] <- "Down"
myData$Pitch3 <- rollapply(myData$pitch, 3, sum, fill = NA, align = "left")
myData$Angle[myData$Pitch3 > upPitch] <- "Up"
myData$Angle[myData$WBF > flight] <- "Flying"
table(myData$Angle)

# make groups of data where bird is going up, down, or flying
myData$Angle <- filterClass(myData$Angle, 2)
myData$Session <- getSessions(myData$Angle, Inf)

# Find the starts of dives where birds are going down and stroking
myData$DiveStarts <- "Unknown"
myData$DiveStarts[which(myData$Angle == "Down" & myData$WBF > startminWBF &
myData$WBF < startmaxWBF)] <- "Diving"

# Make a list of these dive starts
myData$DiveStarts <- filterClass(myData$DiveStarts, 2)
myData$DiveStartID <- getSessions(myData$DiveStarts, Inf)
diveStarts <- summaryBy(FID~ DiveStartID, myData[myData$DiveStarts == "Diving",],
                        FUN = head, n = 1, keep.names = T)[,2]

# Run the dive classification
myData$AccDive <- NA
```

Journal of Experimental Biology • Supplementary information

```
myData$AccDive <- diveDefinition(accdata = myData,
                        diveIDX = diveStarts,
                        maxDive = maxTime,
                        frequency = freq,
                        minWBF = startminWBF,
                        maxWBF = startmaxWBF,
                        changePitch = pitchChange,
                        meanPitch = pitchMean)
accDives <- ifelse(is.na(myData$AccDive), "Unknown", "Diving")
myData$Behaviour <- "Unknown"
myData$Behaviour[!is.na(myData$AccDive)] <- "Diving"
myData$Behaviour[myData$Behaviour == "Unknown" & myData$WBF > 10] <- "Flying"
table(accDives)
```

Journal of Experimental Biology • Supplementary information