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

4
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17
18 **Author contributions:**

19 ES-M, DG, JF and KHE took part in the design and planning of the study. Data collection was
20 undertaken by ES-M, DG, JF, EB-C, MC and SP. AP aided with the analysis of biologged
21 acceleration data. JS processed our blood samples. All authors contributed to manuscript edits.
22

23 **Abstract:**

24

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

43

44 **Introduction**

45 Energy is the most important currency in animal ecology, influencing behavioural
46 decisions, timing of reproduction and, ultimately, fitness (Brown et al. 2004; Grémillet et al.
47 2018). Nonetheless, animal ecologists have developed only a handful of methods for estimating
48 energy costs in the wild, all having strengths and weaknesses (Fort et al., 2011). For example, the
49 doubly labelled water method provides only a single accurate, time-averaged value (Speakman,
50 1997). Heart-rate methods provide values at fine temporal scales, but often involve surgery and
51 can be influenced by cardiovascular adjustments that do not affect energy expenditure (Butler et
52 al., 2004; Green, 2011). In the past two decades, accelerometry has become a popular tool for
53 estimating energy expenditure in wild animals (Elliott, 2016; Wilson et al., 2006), though its
54 origins date back to the early 1960s when laboratory studies began validating the technique on
55 humans (Cavagna et al. 1963; Halsey et al. 2011b). Because the dynamic component of body
56 acceleration should be a robust index of mechanical power output for a known body mass,
57 accelerometers can, in theory, provide an index of nearly instantaneous energy expenditure,
58 assuming that mechanical power is a constant proportion of total energy costs (Wilson et al.,
59 2006). Indeed, studies on several animal taxa have shown the effectiveness of accelerometers as
60 tools for accurately estimating activity-specific energetic costs (Elliott et al., 2013a; Halsey et al.,
61 2011a; Lear et al., 2017; Murchie et al., 2011). Although observation-based time-budgets have
62 provided rough estimates of activity costs, accelerometers are capable of recording activity in
63 greater detail and do not require constant visual contact by observers (Halsey et al., 2011a;
64 Wilson et al., 2006). While other biologgers such as time-depth-temperature tags can also help
65 estimate energy costs in some species, they are often less effective than accelerometers at
66 identifying certain behaviours (Elliott and Gaston, 2014). Furthermore, the continued
67 miniaturization of technology means biologists are able to equip smaller and smaller organisms
68 with accelerometers.

69 While undoubtedly a revolutionary advance in the field of wildlife energetics, nearly two
70 decades of study on a wide variety of species has revealed a few weaknesses with the use of
71 dynamic body acceleration (DBA) as the sole predictor of metabolic rate in some animals. In a
72 recent reappraisal of DBA's use in energetics modeling, Wilson et al. (2020) demonstrated that
73 high and variable non-locomotory energetic costs, such as those linked to thermoregulation, can
74 sometimes mask the relationship between DBA and metabolic rate. Thermal substitution, or the

75 reduction of thermoregulatory costs linked to residual heat produced by muscles during periods
76 of elevated activity (Lovvorn, 2007), can also significantly change the nature of the DBA-energy
77 expenditure relationship in cold environments (Wilson et al., 2020). Animals moving through
78 different media or relying on more than one method of locomotion provide another potential
79 pitfall for researchers attempting to correlate overall energy expenditure with DBA. For example,
80 a similar recording of DBA in air and in water could result in very different energy expenditures
81 for an animal moving in both aerial and aquatic habitats. This difference is also exacerbated
82 when movement in each medium results from different locomotory mechanisms. Hence, some
83 behaviours may disproportionately affect recorded DBA without a coinciding change in energy
84 use (Wilson et al., 2020). Therefore, DBA's relationship with energy expenditure can be
85 variable, often requiring context- or activity-specific assessments (Elliott et al. 2013b; Elliott
86 2016).

87 For the reasons outlined above, modeling the energetics of breath-hold divers such as
88 seals, turtles and seabirds using DBA has been particularly challenging (Grémillet et al., 2018;
89 Halsey et al., 2011b; Halsey et al., 2011c). Notably, dive costs tend to increase non-linearly with
90 lower oxygen consumption rates near the end of long dives as individuals suppress non-essential
91 functions, reduce core temperature and shunt blood directly to arteries (Elliott et al., 2013b;
92 Halsey et al., 2011c; Meir et al., 2008; Niizuma et al., 2007). Additionally, oxygen consumption
93 at the level of the muscle and respiratory system are uncoupled in time during dives (Butler,
94 2006). Thus, although DBA accurately predicts energy expenditure in flying and running animals
95 (Bishop et al., 2015; Halsey et al., 2011a; Wilson et al., 2006), relationships in diving marine
96 vertebrates are often weak without the addition of other model parameters (Halsey, 2017; Rosen
97 et al., 2017; Wilson et al., 2020). Several studies on diving seabirds have shown that
98 accelerometers can predict costs remarkably well in the wild (Elliott et al., 2013a,b; Hicks et al.,
99 2017 and 2020; Stothart et al., 2016; Sutton et al., 2021). However, several of these studies were
100 focused on flightless species, while others were on relatively large (>1 kg), deep-diving species
101 where thermoregulatory and other non-mechanical dive costs may be straightforward to model.
102 For instance, in one species, the fit was better when dive costs were modeled to decrease
103 exponentially with dive duration (Elliott et al., 2013b). Conversely, the dive energetics of small
104 seabirds are likely to be especially difficult to model using DBA, due to the variable mechanical
105 costs associated with buoyancy and their large surface area to volume ratio leading to

106 particularly high thermoregulatory costs when diving in cold water (Gabrielsen et al., 1991;
107 Lovvorn and Jones, 1991; Lovvorn et al., 2004; Wilson et al., 1992).

108 Dovekies (or little auks, *Alle alle*) are small Arctic-breeding seabirds in the family
109 Alcidae. Their abundance makes them key components of many Arctic ecosystems, both as
110 ecosystem engineers and as prey for terrestrial and avian predators (Burnham and Burnham,
111 2005; González-Bergonzoni et al., 2017). As one of the smallest diving marine endotherms (only
112 the *Aethia* auklets and *Pelecanoides* diving-petrels are slightly smaller), dovekies are also an
113 important species from an energetic standpoint, and though their metabolism has been studied in
114 the past, the specific energetic costs of flying and diving remain unknown (Gabrielsen et al.,
115 1991; Harding et al., 2009a; Harding et al., 2009b; Welcker et al., 2009). Dovekies are diving
116 seabirds that feed on a variety of zooplankton, including fish larvae, euphausiids and their
117 primary prey, copepods (Fort et al., 2010). Given that the ranges of their preferred prey, *Calanus*
118 *glacialis*, *Calanus finmarchicus* and *Calanus hyperboreus* are shifting northward due to climate
119 change (Beaugrand et al., 2009), dovekies will likely have to switch to a less nutritious species or
120 increase foraging effort, both of which may increase daily energy expenditure (Amélineau et al.,
121 2016; Grémillet et al., 2012). So far, dovekies have shown a remarkable resilience to the shift,
122 but their ability to buffer its effects may be reaching its limit (Amélineau et al., 2019; Grémillet
123 et al., 2012; Harding et al., 2009b). Understanding dovekie energetics is key to forecasting their
124 current and future responses to global change.

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

137

138 **Methods**

139

140 *Study Area & Data Collection*

141 Dovekies were studied at Ukaleqarteq (Kap Höegh), East Greenland (70° 43' N, 21° 33
142 W) during the 2017 and 2018 breeding seasons. In total, 89 individuals (35 in 2017 and 54 in
143 2018) were captured using a variety of methods including noose carpets and lassos placed on the
144 rocks surrounding their nests. Each dovekie was injected intraperitoneally with 0.3 mL (2017) or
145 0.45 mL (2018) of doubly-labelled water (the dosage was increased in 2018 to extend the
146 recapture window; Speakman, 1997). Of those birds, we taped small triaxial accelerometers
147 (Axy4, Technosmart, Italy; 3.4g including tubing and tape) to the breast feathers of 60 birds to
148 record their activity. Recaptures began approximately 20 hours after the birds were released.
149 Body measurements (flattened wing, tarsus and beak length) were taken for each dovekie
150 following final blood sampling.

151

152 *Energy Expenditure*

153 To estimate the average energy expenditure of each of our birds, we used the doubly
154 labeled water (DLW) method (Speakman, 1997; Welcker et al., 2009). This method estimates
155 carbon-dioxide production using the differential decline of heavy isotopes of hydrogen and
156 oxygen in the body. The two-sample approach involves taking a blood sample at the beginning
157 and at the end of a measurement period, while the one-sample approach involves taking only a
158 final sample and interpolating the initial enrichments of ¹⁸oxygen and deuterium. We used the
159 one-sample method for all our accelerometer-equipped birds to reduce handling time (handling
160 time: ~10-15 minutes). The increased handling time associated with the two-sample approach is
161 known to alter behaviour, and therefore energy expenditure, in other seabirds (Schultner et al.,
162 2010). As such, the two-sample approach was reserved for the birds not being equipped with
163 accelerometers and whose initial isotope enrichments could be used to interpolate the initial
164 enrichments of the one-sample birds using body mass ($R^2 = 0.68-0.74$ between isotopes and
165 mass depending on year; see data appendix).

166 Immediately following capture, all birds were weighed in an opaque breathable bag using
167 a small hanging scale and then injected intraperitoneally with DLW (65% H₂O¹⁸; 35% D₂O). The

168 one-sample birds were equipped with an accelerometer, marked with dye, and then released.
169 Following the DLW injection, we placed the two-sample birds in the shade for one hour to allow
170 the DLW to equilibrate with the body water. After the hour had elapsed, an initial blood sample
171 was taken from each bird's brachial vein, following which, the birds were marked with dye and
172 released. All birds were recaptured for a final weighing and blood sample after 15 to 50 hours
173 (accelerometers were removed prior to weighing). The isotopic enrichments of blood samples
174 were measured using an isotopic water analyzer (Los Gatos, San Jose, USA). We calculated the
175 amount of carbon dioxide produced by individuals over the course of each deployment using the
176 plateau method (See Speakman, 1997 for details on calculations and supporting theory). To
177 estimate energy expenditure, we converted these values into kilojoules using a conversion
178 coefficient of 27.97 J/mL of CO₂ (Welcker et al., 2009). Daily energy expenditure (DEE) was
179 then estimated by dividing total energy expenditure by the deployment duration for each
180 dovekie. An unbalanced two-way ANOVA was performed using the car package in R (Fox and
181 Weisberg, 2019) to test for differences in mean DEE estimated for dovekies across sampling
182 years and DLW sampling approaches (i.e. one- and two-sample). Normality and homogeneity of
183 variance was assessed visually using standard residual plots (Q-Q plot and residuals vs. fitted
184 plot).

185

186 *Accelerometry & Activity Costs*

187 Raw acceleration data in the surge, heave and sway axes were recorded at a sampling rate
188 of 50 Hz and used to calculate stroke frequency and pitch (i.e. body angle) in R using code
189 adapted from Patterson et al.'s work on thick-billed murrelets (2019). Specifically, a fast Fourier
190 transform, applied over a 5-second moving window, was used to determine the peak frequency in
191 the heave axis (Patterson et al., 2019). Flights were identified as any period with a stroke
192 frequency greater than 10 Hz. Pitch was calculated using a 2-second moving average of the
193 heave, sway, and surge axes. To account for differences among individuals and the placement of
194 accelerometers on birds, pitch values were standardized to 0 during flights (Patterson et al.,
195 2019). A 3-second moving window of pitch was used to define periods when the dovekie was
196 descending (pitch < -45°) or ascending (pitch >45°).

197 As we did not have a pressure sensor, the start of likely dives was determined based on
198 periods when the dovekie was descending for at least 2 seconds, with a stroke frequency between

199 1 and 6 Hz. During the bottom phase of a dive, the dovekie uses either dive strokes or changes in
200 pitch to maintain buoyancy and search for prey. From the start of a likely dive, we identified the
201 next time where the bird was not ascending or descending, did not have a stroke frequency
202 between 1 – 6 Hz, and change in pitch was less than 10° (i.e. assumed to be back at the surface).
203 If these conditions were not met within 120 seconds (the presumed maximum dive duration),
204 then the end of the dive was defined as 120 seconds after the dive start. These diving periods
205 were also identified visually in a subset of deployments in order to verify the validity of the
206 automatic classifications and were found to be in close agreement (Cohen’s kappa coefficient =
207 0.82 ±0.08, n=10). As such, only automatically defined dives were used in all further analyses.
208 Automatic dive classification R-code is available in the Appendix.

209
210 To estimate energetic costs in dovekies, we compared several models using activity-
211 specific time-budgets and dynamic body acceleration as predictors. We began by conducting
212 multiple regression analyses with activity-specific time budgets (percentages of total deployment
213 time) as explanatory variables and mass-specific DEE as the response variable. We opted to use
214 mass-specific DEE instead of absolute DEE to facilitate comparisons with the dynamic body
215 acceleration models described in the next section (further justification is available in the SI
216 appendix). Since one of the primary objectives of the study was to estimate flight and dive costs,
217 three activity categories were initially selected for analysis: flying, diving and other (resting,
218 walking, etc).

$$219 \quad \text{DEE} = a(\% \text{Time}_{\text{fly}}) + b(\% \text{Time}_{\text{dive}}) + c(\% \text{Time}_{\text{other}}) \quad (\text{Model 1})$$

220
221
222 The intercept was forced through zero to account for the fact that no energy is expended when no
223 time has elapsed (this also applies to the other time-budget models described below). The output
224 of the multiple regression analysis was then used to estimate the activity-specific costs of flying
225 and diving in dovekies.

226 Other model variants were subsequently tested against our basic model to see which best
227 explained DEE. Several variants used combinations of the basic time budget categories outlined
228 above as explanatory variables (Models 2-4), while another split the “other” category into
229 “resting on land” and “unknown” (Model 5; details available in the SI appendix). Unfortunately,

230 we could not further breakdown the “unknown” category into other potentially important
231 behaviours using acceleration data only, a limitation of working with such a small species where
232 larger tags cause behavioural disruption. Since dive costs could have declined exponentially with
233 dive duration (e.g. Elliott et al., 2013b), as measured in penguins and modelled in larger auks, we
234 also tested a model variant that replaced the percentage of time spent diving with an exponential
235 cost function for each dive (Model 6; details available in SI appendix). We then considered
236 models incorporating overall dynamic body acceleration (ODBA) as a possible predictor of
237 DEE. ODBA represents the summed dynamic acceleration across all three axes of movement.
238 Dynamic acceleration was calculated by subtracting the static component of acceleration (i.e.
239 that associated with gravity and body position) from the raw acceleration for each axis. Static
240 acceleration was calculated by applying a 2-second rolling mean to the raw acceleration data in
241 order to remove any signal resulting from the animal’s movement (e.g. wingbeats). As time’s
242 effect on summed ODBA inflates its importance in energetics models (Halsey, 2017), the first
243 ODBA model variant (Model 7) used overall time-averaged ODBA as the sole explanatory
244 variable. The second ODBA model variant (Model 8) multiplied mean activity-specific ODBA
245 by the time-budget percentages for each behavioural category to see if incorporating ODBA
246 improved the fit of the basic time-budget model (i.e. Model 1).

247

$$248 \text{ DEE} = d(\% \text{Time}_{\text{fly}} * \text{ODBA}_{\text{fly}}) + e(\% \text{Time}_{\text{dive}} * \text{ODBA}_{\text{dive}}) + f(\% \text{Time}_{\text{other}} \text{ODBA}_{\text{other}}) \quad (\text{Model 8})$$

249

250 We selected the best model(s) using Akaike’s Information Criterion (AIC) which
251 penalizes unnecessarily complex models (Table 1). The model with the lowest AIC score was
252 considered best, and models with a $\Delta\text{AIC} < 2$ were assumed equivalent to the best model and
253 discussed in further detail throughout (Symonds and Moussalli, 2011). Using the coefficients
254 resulting from selected models, we calculated predicted DEE and plotted it against doubly
255 labeled water derived DEE. We then performed a reduced major axis (RMA) regression using
256 the *smatr* package for R (Warton et al. 2012) to check whether predicted DEE was in close
257 agreement with the doubly labeled water derived DEE estimates that our models were based on.
258 To illustrate the potential relationship between DEE and ODBA (i.e. Model 7), doubly labeled
259 water derived DEE was plotted against mean ODBA, revealing an obvious gap between points
260 for dovekeys tagged in 2017 and those tagged in 2018. Since sampling year could have

261 influenced the relationship between mean ODBA and DEE_{dlw} , we subsequently conducted a
262 linear regression analysis on both the pooled dataset (2017 and 2018, Model 7) and the dataset
263 for dovekeys tagged in 2017 only. We did not analyse the 2018 dataset independently given the
264 small sample size for that year. Differences in mean ODBA across our three basic behaviour
265 categories (flight, diving and other) were assessed using a one-way ANOVA followed by a
266 Tukey post-hoc test. Given the small sample sizes for each test group, residual plots (Q-Q and
267 Residuals vs. fitted) were used to check the normality and homogeneity of variance assumptions
268 instead of a formal test. All statistical analyses were conducted in R (R Core Team, 2018).

269

270 *Allometry of Stroke Frequency*

271 Density plots were used to identify the dominant stroke frequency exhibited by
272 individuals during locomotion in the air and underwater. We then tested for an intra-specific
273 linear relationship between $\log_{10}(\text{stroke frequency})$ and $\log_{10}(\text{mass})$ in dovekeys while flying and
274 diving. In an attempt to explain some of the residual variation surrounding these relationships,
275 we regressed residuals against wing-loading, which was calculated for each bird by dividing their
276 mass by the area of their wings (approximated by wing-length squared). We continued to plot the
277 mean dominant stroke frequency observed across all sampled individuals with literature values
278 for other vertebrates (Sato et al., 2007), as well as for Alcids specifically (Elliott et al., 2004). If a
279 species was represented in both studies, we chose the value provided in Sato's paper which relied
280 on accelerometer derived estimates instead of video analysis (Literature values presented in
281 Supplementary Table 1). We then conducted a linear regression analysis on \log_{10} -transformed
282 mass and stroke frequency to derive inter-specific allometric scaling relationships for stroke
283 frequency in diving and flying Alcids and compared them to those published by Elliott et al.
284 (2004) and Sato et al. (2007) for Alcids and marine vertebrates respectively.

285

286 **Results**

287 Due to weather and logistics constraints, 54% of the 35 deployed dovekeys were recaptured in
288 2017 and only 31% of the 54 birds deployed in 2018. Of these, several were caught outside of
289 the timeframe when DLW analysis is possible. We estimated DEE in a total of 24 birds across
290 both sampling years (14 one-sample and 10 two-sample individuals). Of the recaptured
291 individuals for whom DEE could not be estimated, we were able to recover acceleration data

292 from an additional six birds, bringing the total number of recovered accelerometers from one-
293 sample birds to 20. Average DLW derived daily energy expenditure (DEE) for dovebies in 2017
294 and 2018 was $621 \pm 103 \text{ kJ.d}^{-1}$ and $590 \pm 133 \text{ kJ.d}^{-1}$, respectively (Supplementary Table 2). A
295 two-way ANOVA showed no significant differences between estimates for both sampling years
296 ($p=0.90$, $n=11$ in 2017 and $n=13$ in 2018), nor between those for one- and two-sample birds
297 ($p=0.22$, $n=14$ one-sample and $n=10$ two-sample).

298 Of the eight model variants used to explain DLW-derived DEE, two were selected by
299 comparing AIC values, both of which were time-budget models (Model 1 and Model 2; Table 1).
300 The coefficients resulting from these models provided energetic cost estimates for each
301 behaviour category (Table 2). From Model 1, the estimated flight cost for dovebies was 98 W kg^{-1}
302 $(95\% \text{ CI}= 63\text{-}133 \text{ W kg}^{-1})$ or approximately 7.24 X BMR (using a BMR estimate of 177.9 kJ d^{-1}
303 for dovebies of mean mass = 152.5 g [Gabrielsen et al., 1991]). Our estimated dive cost was 126
304 W kg^{-1} ($95\% \text{ CI}= 86\text{-}167 \text{ W kg}^{-1}$) or approximately 9.37 X BMR. Model 2, which combined time
305 budgets for flying and diving, estimated a combined cost of 110 W kg^{-1} ($95\% \text{ CI}=86\text{-}135 \text{ W kg}^{-1}$)
306 for these behaviours (i.e. 8.16 X BMR). Figures 1A and 1B illustrate the utility of our model
307 coefficients with regards to predicting DLW-derived DEE (RMA regression with $n=13$, Model 1:
308 $R^2= 0.77$, $p=7.48 \times 10^{-05}$, Fig.1A, and Model 2: $R^2= 0.74$, $p=0.000145$, Fig.1B). Models
309 incorporating ODBA (Models 7 and 8) did not improve on time-budget models, nor did
310 replacing percent of time spent diving with an exponential cost function (Model 6).

311 The tagged dovebies used in our energy expenditure modeling exhibited an overall mean
312 ODBA of $0.41 \text{ g s}^{-1} \pm 0.06$ (SD), while activity-specific ODBA was $0.71 \text{ g s}^{-1} \pm 0.06$ for flight,
313 $0.67 \text{ g s}^{-1} \pm 0.07$ for diving and 0.25 ± 0.08 for the other behavioural category (Table 3). A one-
314 way ANOVA showed there was significant differences in mean ODBA across behaviours ($F_{2,36}$
315 $=167.1$, $p=0.000$). A Tukey post-hoc test revealed that mean ODBA during flight and diving
316 were not significantly different from each other ($p= 0.270$), but both differed significantly from
317 mean ODBA during “other” behaviours ($p=0.000$). We did not find a significant relationship
318 between DEE and mean ODBA for the 2017 and 2018 pooled dataset ($p= 0.734$, $n=13$, Fig. 2).
319 However, a weak linear relationship was found when only using data for dovebies tagged in
320 2017 ($R^2 = 0.41$, $p= 0.0478$, $n=10$).

321

322 Stroke frequency varied significantly with mass across individual dovekeys during flight
323 (p= 0.00641, $R^2=0.35$; Fig. 3A), but not diving (p= 0.116; Fig. 3B). However, confidence
324 intervals for the allometric exponent for flight were quite broad, indicating a high level of
325 uncertainty surrounding the estimate (exponent = -0.42, 95% CI= -0.70 to -0.13). Wing loading
326 did not explain residual variation (p=0.155). Combining our mean dominant stroke frequency for
327 dovekeys with published values for other species of Alcid yielded an allometric scaling exponent
328 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 -
329 0.27 ± 0.033 for diving (p= 0.00367, $R^2=0.96$, n=5, 95% CI = -0.38 to -0.17, Fig. 4B).

330 **Discussion**

331

332 In accordance with our expectations for a small shallow-diving endotherm in the Arctic,
333 time-averaged ODBA was not an effective predictor of DEE, though a weak relationship was
334 found when considering data for 2017 only. Similarly, the addition of activity-specific ODBA to
335 basic time budget models did not improve their ability to explain variation in DEE. In fact, our
336 two best models used only accelerometer-derived time budgets as explanatory variables. Despite
337 recording similar ODBA in flying and diving dovekeys (Table 3), time-budget models suggested
338 the energetic cost of diving could be almost 30% higher than that of flying (7.24 BMR for flight
339 and 9.37 BMR for diving). Put together, these findings suggest that high non-mechanical costs
340 such as thermoregulation during dives are weakening the relationship between ODBA and DEE
341 (Wilson et al., 2020). Furthermore, while dive costs were relatively high compared to flight in
342 dovekeys, their average stroke frequency while diving was consistent with inter-species
343 allometric scaling relationships. Thus, dovekeys represent an empirical example of how the link
344 between DBA metrics and energy expenditure is weaker in species apparently facing greater
345 proportions of non-mechanical costs and which exhibit multiple movement modes (Wilson et al.,
346 2020).

347

348 *Daily Energy Expenditure*

349

350 Despite rapid environmental changes in the Arctic, DEE estimates for nesting dovekeys in
351 2017 and 2018 in East Greenland were comparable to previous estimates going back ~30 years
352 for birds breeding at the same site and in Svalbard (~600-760 kJ/day; Gabrielsen et al., 1991;
353 Harding et al., 2009b; Welcker et al., 2009). Thermoregulatory energy savings resulting from
354 warming temperatures may be offsetting losses associated with changing foraging dynamics,
355 allowing dovekeys to buffer the effects of climate change in East Greenland (Grémillet et al.
356 2012). However, as prey dynamics continue to shift with increasing temperatures, dovekeys may
357 soon face increased energetic demands that exceed their capacity to buffer, eventually leading to
358 decreases in fitness (Kidawa et al. 2015; Amélineau et al. 2019). As such, it is essential that we
359 continue to monitor the behaviour, energetics and breeding success of these abundant Arctic
360 seabirds. Going forward, the models presented here can be used to easily estimate energy

361 expenditure using basic time-budgets derived from accelerometers or other tag types if they can
362 identify periods of flight and diving.

363

364 *Activity Costs*

365

366 Until now, only rough estimates of the energetic costs of flying and diving existed for
367 dovebies and these were based on allometric relationships or biomechanical modeling (i.e. the
368 Pennycuick model; Pennycuick 1989). Prior to the availability of fine scale movement data made
369 possible through the use of accelerometers, diving and flying were estimated in dovebies to cost
370 between 4.8 and 11.6 X BMR (Fort et al., 2009; Gabrielsen et al., 1991). While both our
371 estimated flight and dive costs fell within that range (7.24 and 9.37 X BMR), dive costs were
372 relatively high compared to flight costs. Some species are known to trade-off time budgets for
373 energetically costly behaviours in order to minimize overall costs (Elliott et al 2013), which may
374 explain why time budgets for flight and diving were negatively correlated across all
375 accelerometer-equipped individuals in our study ($r = -0.61$, $n = 20$, details available in SI
376 appendix). Regardless, our estimated activity costs can be used to inform our current
377 understanding of the long-term health of dovebie populations globally by improving existing
378 models (e.g. Clairbaux et al. 2019).

379 The flight costs derived in this study support the idea that high wing-loading in dovebies is
380 resulting in high energetic costs during flapping-flight. For instance, these estimates are almost
381 double that of the similarly sized sooty tern (*Sterna fuscata*), which has a much lower wing-
382 loading than the dovebie (Flint and Nagy, 1984). Even so, when compared to the flight costs of
383 the largest auk species, the thick-billed murre (*Uria lomvia*, 31 X BMR; Elliott et al., 2013b),
384 dovebies have relatively low flight costs. This is almost certainly because thick-billed murres
385 have roughly two times higher wing-loading than dovebies (Gabrielsen et al. 1991; Elliott et al.
386 2013b), and induced flight costs increase non-linearly with wing-loading (proportionate to
387 $(\text{Mass}/\text{wingspan})^2$; Pennycuick, 2008). The effect of mass has been widely studied and, though a
388 level of variability exists, flight costs tend to increase with mass both inter- and intra-specifically
389 in birds (Videler, 2006). This pattern is obvious when comparing the flight costs of one of the
390 smallest Alcids (the dovebie, 98 W kg^{-1}) with the largest (the thick-billed murre, 146 W kg^{-1} ;

391 Elliott et al., 2013b) but may also be present among individual dovekies of varying mass, though
392 this is beyond the scope of the present study.

393 As expected, dovekies had relatively high dive costs compared to other species. Though
394 these small seabirds have short dive-adapted wings, they are still longer (relative to body size)
395 than in other Alcids, like the thick-billed murre whose relative dive costs are typically lower than
396 in dovekies (~40W/kg for an average length dive, Elliott et al., 2013b). Longer wings increase
397 hydrodynamic drag when moving through the water and this translates to increases in the
398 energetic requirements of diving (Elliott et al., 2007). On average, dovekies also exhibit much
399 shorter and shallower dives than thick-billed murres and this likely means that they face much
400 higher costs linked to buoyancy when diving (Elliott et al., 2007; Harding et al., 2009a; Lovvorn
401 et al., 2004). Buoyancy is predicted to decline exponentially with depth and so shallow divers
402 must spend more time and energy overcoming it (Lovvorn et al., 2004; Wilson et al., 1992).
403 Dovekies have been recorded making up to 240 individual dives per day at an average depth of
404 10m (Harding et al., 2009a), and so, the cost of buoyancy is likely a large contributor to the
405 particularly high dive costs observed in these birds.

406 Thermoregulatory costs are also likely higher in diving dovekies than in thick-billed murres
407 because of their relatively large surface area to volume ratio (Gabrielsen et al., 1991; Gardner et
408 al., 2011). Small endotherms lose heat much faster in water than in air, leading to significantly
409 higher metabolic rates in water (Croll and McLaren, 1993). These thermoregulatory costs
410 increase steeply as temperatures drop; something which has been demonstrated in many seabirds
411 resting on water, including three other Alcids (Croll and McLaren, 1993; Richman and Lovvorn,
412 2011). While thermal substitution can offset some of these costs by recycling heat generated by
413 muscles during dives (Lovvorn, 2007), thermoregulatory costs are likely still high for small
414 Arctic species diving in near-freezing waters. On the other hand, as shallow divers (average
415 depth ~10 m; Harding et al., 2009b), dovekies may benefit from the air trapped in their feathers
416 whose insulative properties would diminish significantly at greater depth (Lovvorn, 2007).
417 Regardless, the high non-mechanical costs incurred by diving dovekies explains the elevated
418 dive costs predicted here, as well as the decoupling of DBA from energy expenditure observed in
419 these birds (Halsey et al., 2011b; Wilson et al., 2020).

420 The morphological and physiological characteristics of a species are not the only factors that
421 can influence activity costs. Environmental conditions can also have significant effects on the

422 energetic costs associated with specific behaviours and could explain some of the variation
423 observed in our model. For example, a study undertaken on two species of seabird found that
424 flight costs increased with increasing head winds (Elliott et al., 2014). As such, differences in the
425 wind regimes experienced by the dovebies deployed in 2017 and 2018 could have led to
426 differences in the relative energetic costs associated with flight in each cohort, and previous
427 research on dovebies has shown that DEE increases with wind speed in this species (Gabrielsen
428 et al., 1991). Unfortunately, wind speed could not be measured at the study site during those two
429 years. Similarly, interannual differences in sea surface temperature could have affected the
430 thermoregulatory dive costs incurred by dovebies in both sampling years. For example, sea
431 surface temperatures in the colony's foraging range were higher in 2018 (mean SST for July and
432 August = 1.70 ± 0.39 °C) than in 2017 (0.72 ± 0.47 °C), consistent with DEE in 2018 being
433 lower than expected based on activity levels alone (Fig. 1; refer to the appendix for details on
434 how bimonthly mean SSTs were derived).

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

445

446 *Allometry of Stroke Frequency*

447

448 Dominant stroke frequency during flight varied across individual dovebies with $\text{Mass}^{-0.42}$,
449 higher than the predicted inter- and intra-specific exponent of between $-1/6$ and $-1/3$, but lower
450 than the $-1/2$ exponent predicted for intra-individual stroke frequency allometry in birds (Berg et
451 al., 2019; Pennycuick, 2008). Inter-individual variation in wingspan and wing area may be
452 relatively small across dovebies, leading to an allometric scaling exponent that approaches $-1/2$.

453 This could be the case if mass differences across individuals are resulting from varying fat
454 reserves instead of overall differences in body size (Pennycuick, 2008). While nesting dovekies
455 may benefit from large fat reserves, they also likely incur higher activity costs associated with
456 increased stroke frequency during flight (Taylor, 1994). However, wing loading did not explain
457 the high degree of variation surrounding the relationship between body mass and stroke
458 frequency in flying dovekies nor the lack of a significant relationship for diving dovekies,
459 suggesting other factors are at play here.

460 We combined the mean stroke frequency of flying and diving dovekies with literature data
461 for other Alcids to assess the inter-specific allometry of stroke frequency in this family with the
462 inclusion of one of its smallest members. Despite having lower mass-specific stroke frequencies
463 than other swimming vertebrate taxa, the scaling exponent (-0.27) obtained for diving Alcids was
464 nearly identical to that observed across birds, fish, reptiles and mammals in a previous study (-
465 0.29, Sato et al. 2007; Fig. 4B). This supports the idea that a morphological trade-off between
466 efficient locomotion in air and water affects the intercept and not the slope of log-log
467 relationships for stroke frequency allometry in diving Alcids (Sato et al., 2007). Our estimated
468 allometric exponent for flight in Alcids (-0.22) agrees closely with the exponent published by
469 Elliott et al. (2004) despite the addition of data points for three species of Alcid not present in the
470 original dataset. These added species included the largest and smallest studied auks (i.e. the
471 dovekie and the thick billed murre). Dovekie stroke frequency was well predicted by our derived
472 allometric relationships for flight and diving in Alcids, implying once again that their unusually
473 high dive costs are not being driven by mechanical costs alone.

474

475

476 *Conclusion*

477

478 The use of accelerometers has greatly enhanced our ability to study the fine-scale behaviour
479 and energetics of wildlife. However, our results support the hypothesis that dynamic body
480 acceleration alone is not an effective predictor of daily energy expenditure in species
481 experiencing high non-mechanical energetic costs and using multiple movement modes (Wilson
482 et al., 2020). Nevertheless, acceleration derived time-budgets were effective at providing
483 estimates of energy expenditure in dovekies, and revealed that dive costs are particularly high in

484 this species. Since the DLW method is challenging to perform in species like dovekies,
485 accelerometers can be used to study their energetics going forward. Additionally, the use of
486 accelerometer-derived information in ecological modeling is not restricted to energetics alone.
487 The detailed data provided by these tags can also be used to parametrize other models
488 forecasting the fitness, distribution and population dynamics of species faced with the mounting
489 pressures of global change (e.g. Grémillet et al. 2018).

490
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492

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507

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510 for other vertebrate species were acquired from published research by Sato et al. (2007) and
511 Elliott et al. (2004).

512

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Tables

515

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

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

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522 **Table 2:** Output of the best models (Δ AIC<2) for explaining doubly-labeled water estimates of
 523 mass-specific daily energy expenditure in doves equipped with accelerometers. 95%
 524 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) |

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*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⁻¹g⁻¹).

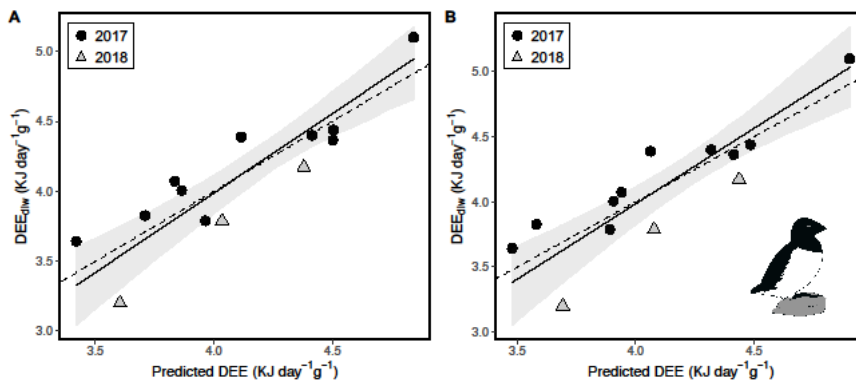
**Activity cost estimates presented as multiples of basal metabolic rate (BMR) using a previously published value (BMR = 177.9 KJ d⁻¹, n=16, at mean body mass = 152.5 g; Gabrielsen et al. 1991).

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

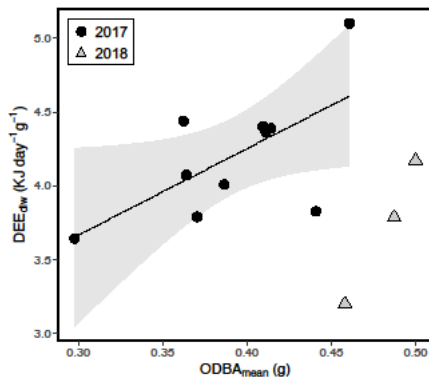
| Year | Time averaged ODBA (g s^{-1}) | | | | | | Other | $\pm\text{SD}$ | n |
|-------------|--|------------------------------|-------------|------------------------------|-------------|------------------------------|-------------|------------------------------|-----------|
| | Mean | $\pm\text{SD}$ | Flying | $\pm\text{SD}$ | Diving | $\pm\text{SD}$ | | | |
| 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 |

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Figures

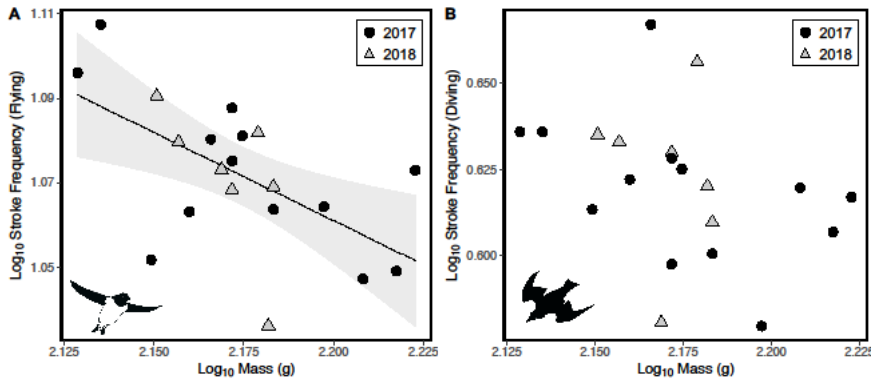


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 542 **Figure 1:** Time-budget predicted daily energy expenditure for the two model variants with
 543 $\Delta\text{AIC} < 2$ (Model 1 [A] and Model 2 [B]) plotted against doubly labeled water derived estimates
 544 of daily energy expenditure (DEE_{dlw}). Black lines represent the output of a reduced major axis
 545 regression with shaded regions depicting 95% confidence intervals (n=13, Model 1: $R^2 = 0.77$,
 546 $p < 0.0001$, $\text{DEE}_{\text{dlw}} = 1.14(\text{Predicted DEE}) - 0.56$; Model 2: $R^2 = 0.74$, $p < 0.001$, $\text{DEE}_{\text{dlw}} =$
 547 $1.16(\text{Predicted DEE}) - 0.65$); Dashed lines depict the lines of equality (i.e. 1:1 relationship).
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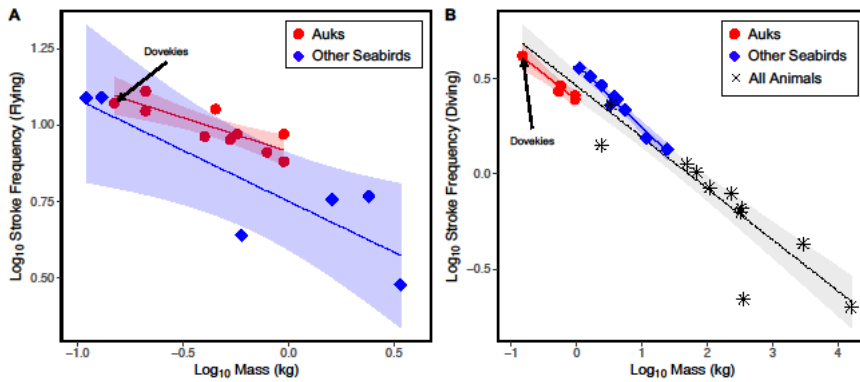


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 550 **Figure 2:** Doubly labeled water derived estimates of daily energy expenditure (DEE_{dlw}) plotted
 551 against time-averaged overall dynamic body acceleration ($\text{ODBA}_{\text{mean}}$). There was a weak

552 significant linear relationship between DEE_{dlw} and $ODBA_{mean}$ for dovekies tagged in 2017
 553 ($R^2=0.41$, $p<0.05$, $n=10$; $DEE_{dlw}= 5.87(ODBA_{mean})+ 1.90$; shaded region represents the 95%
 554 confidence intervals), but none for the combined datasets of 2017 and 2018 ($p>0.05$, $n=13$).
 555



556 **Figure 3:** Dominant stroke frequencies (Hz) plotted against mass for (A) flying (Stoke frequency
 557 = $94.914[Mass]^{-0.416}$; $p< 0.01$, $R^2= 0.35$, $n=20$) and (B) diving dovekies (no significant
 558 relationship).
 559
 560



561 **Figure 4:** Mean stroke frequencies (Hz) plotted against mass for (A) flying and (B) diving
 562 animals. In panel (B), the “All animals” trendline is inclusive of “Auks” and “Other Seabirds”.
 563 All data points aside from those for dovekies are derived from previous research by Sato et al.
 564 (2007) and Elliott et al. (2004). Stroke frequency varied significantly with mass across auks
 565 during flight (Stoke frequency = $8.188[Mass]^{-0.221}$; $p<0.01$, $R^2=0.73$, $n=8$), and while diving
 566 (Stroke frequency = $2.4453[Mass]^{-0.274}$; $p<0.01$, $R^2=0.96$, $n=5$). Data for dovekies are indicated
 567 by black arrows.
 568
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