



HAL
open science

Innovative Use of Depth Data to Estimate Energy Intake and Expenditure in Adélie Penguins

Benjamin Dupuis, Akiko Kato, Olivia Hicks, Danuta Wisniewska, Coline Marciau, Frédéric Angelier, Yan Ropert-Coudert, Marianna Chimienti

► **To cite this version:**

Benjamin Dupuis, Akiko Kato, Olivia Hicks, Danuta Wisniewska, Coline Marciau, et al.. Innovative Use of Depth Data to Estimate Energy Intake and Expenditure in Adélie Penguins. *Journal of Experimental Biology*, 2024, 10.1101/2024.07.02.601650 . hal-04784622

HAL Id: hal-04784622

<https://hal.science/hal-04784622v1>

Submitted on 15 Nov 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Title:**

2 "Innovative Use of Depth Data to Estimate Energy Intake and Expenditure in Adélie
3 Penguins"

4 **Running title:**

5 TDRs estimate energetics of penguins

6

7 **Authors:**

8 Benjamin Dupuis*¹, Akiko Kato¹, Olivia Hicks^{1,2}, Danuta M. Wisniewska^{1,3}, Coline
9 Marciau^{1,4}, Frederic Angelier¹, Yan Ropert-Coudert¹, Marianna Chimienti¹.

10

11 **Affiliations:**

12 1. Centre d'Etudes Biologiques de Chizé, CNRS, La Rochelle Université, UMR 7372,
13 Villiers-en-Bois, France.

14 2. School of Oceans science, Bangor University, Menai Bridge LL59 5AB, UK

15 3. Sound Communication and Behavior Group, Department of Biology, University of
16 Southern Denmark, Odense M, Denmark

17 4. Institute For Marine and Antarctic Studies, University of Tasmania, Hobart,
18 Australia

19

20 *Corresponding author email: Benjamin.dupuis@ens-lyon.org

21 **Keywords:**

22 Foraging activity, time-depth recorders, energy expenditure, diving behaviour, marine

23 predator, machine learning

24

25 **Summary statement:**

26 Using machine learning, we estimated energy expenditure and foraging activity of
27 free-ranging Adélie penguins using depth data recorded with bio-logging devices.

28

29 **Abstract:**

30 Energy governs species' life histories and pace of living, requiring individuals to make
31 trade-offs. However, measuring energetic parameters in the wild is challenging, often
32 resulting in data collected from heterogeneous sources. This complicates
33 comprehensive analysis and hampers transferability within and across case studies.
34 We present a novel framework, combining information obtained from eco-physiology
35 and bio-logging techniques, to estimate both energy expended and acquired on 48
36 Adélie penguins (*Pygoscelis adeliae*) during the chick-rearing stage.

37 We employ the machine learning algorithm random forest (RF) to predict
38 accelerometry-estimated foraging behaviour using depth data (our proxy for energy
39 acquisition). We also build a time-activity model calibrated with doubly labelled water
40 data to estimate energy expenditure.

41 Using depth-derived time spent diving and amount of vertical movement in the sub-
42 surface phase, we accurately predict energy expenditure ($R^2 = 0.70$). Movement
43 metrics derived from depth data modelled with the RF algorithm were able to
44 accurately (accuracy = 0.82) detect the same foraging behaviour predicted from
45 accelerometry. The RF more accurately predicted accelerometry-estimated time
46 spent foraging ($R^2 = 0.81$) compared to historical proxies like number of undulations
47 ($R^2 = 0.51$) or dive bottom duration ($R^2 = 0.31$).

48 The proposed framework is accurate, reliable and simple to implement, enabling to
49 couple energy intake and expenditure, which is crucial to further assess individual
50 trade-offs. We provide universal guidelines for predicting these parameters based on
51 widely used bio-logging technology in marine species. Our work allows us to revisit
52 historical data, to study how long-term environmental changes affect animals'
53 energetics.

54 1. INTRODUCTION

55 Energy is the fundamental currency shaping animals' life-history strategies (Burger et
56 al., 2019; Kressler et al., 2023; Pontzer and McGrosky, 2022). Individuals within
57 populations acquire and spend energy to fuel activities such as movement, body
58 maintenance, thermoregulation and reproduction (Gower et al., 2008; Noakes et al.,
59 2013; Steinhart et al., 2005). As energy acquisition from the environment is limited,
60 individuals' performances and trade-offs in energy allocation directly impacts life-
61 histories traits like survival and reproduction, and therefore fitness and population
62 processes (Brown et al., 2004; Mogensen and Post, 2012; Morano et al., 2013). In
63 addition to fuelling all physiological processes, energy acquisition (i.e. foraging) itself
64 requires physical activity and therefore energy expenditure (Pontzer and McGrosky,
65 2022). Environmental variations in biotic (e.g., in prey availability) and abiotic factors,
66 and animal internal states can affect how energy is spent and acquired, and lead to
67 adjustments in foraging strategies (Byrne et al., 2022; Chevallay et al., 2022; Egert-
68 Berg et al., 2021).

69 In order to understand individual trade-offs, it is important to consider both energy
70 acquisition and expenditure within the same framework. Yet, simultaneously
71 measuring energy intake and expenditure in wild animals is challenging. Numerous
72 species forage in areas almost impossible to sample (*i.e.* deep oceans, remote land,
73 sky), making observations difficult. Approaches in eco-physiology, like doubly-
74 labelled water (DLW), respirometry, heart-rate monitors, or oesophagus temperature
75 sensors have proven useful in providing data to validate energy expenditure and
76 intake (Froget et al., 2004; Hicks et al., 2020; Nagy et al., 1999; Ropert-Coudert et
77 al., 2001). However, these approaches are costly, logistically difficult, invasive and,
78 therefore, challenging to consistently use in long-term species monitoring programs.

79 Given the difficulties in simultaneously measuring both energy expenditure and
80 energy acquisition in wild animals, information comes from different data types
81 (English et al., 2024) making long-term analysis or study comparisons difficult.

82 Recent advances in bio-logging technologies allowed researchers to validate the use
83 of accelerometers to accurately estimate animals' energetics across a wide range of
84 taxa and habitats (English et al., 2024; Wilson et al., 2020). Top predators integrate
85 information from the bottom to the top of the food webs. As such, they are
86 recognized as sentinels of global change, and allow understanding the impact of
87 environmental changes on ecosystems (Hazen et al., 2019; Sergio et al., 2008).
88 Marine top predators are of special interest because they live in environments where
89 global changes have rapid and important consequences on ecosystems (Sydeman et
90 al., 2015). They are often both wide-ranging and conspicuous (compared to lower-
91 marine trophic levels) (Hazen et al., 2019). By recording tri-axial body acceleration at
92 high resolution (25-100 Hz) on top predator species such as white sharks (Watanabe
93 et al., 2019), southern elephant seals (Gallon et al., 2013) or penguins (Kokubun et
94 al., 2011), it is possible to detect prey capture attempts and to classify behaviours.
95 Such methodology also allows us to estimate energy expenditure across foraging
96 trips when validated with the DLW technique for example (Chimienti et al., 2016; Del
97 Caño et al., 2021; Hicks et al., 2020). Yet, because of their novelty, historical time
98 series of accelerometer data are often not available.

99 On the contrary, time-depth recorders (TDRs) have been extensively used on diving
100 predators since the 90's (Ropert-Coudert et al., 2009) to reconstruct dive profiles,
101 investigate foraging behaviour, and estimate energy expenditure of diving marine
102 predators (Chappell et al., 1993a, 1993b; Viviant et al., 2014). Despite lower
103 accuracy, data collection via TDRs presents several advantages compared to data

104 collected with accelerometer tags. For instance, TDRs are more suitable for extended
105 recording periods (months or years of continuous recording). TDRs record data at
106 lower resolution (usually 1Hz or coarser) requiring reduced memory space and
107 battery consumption, and do not need to be placed at or near the centre of the mass
108 of the animal like accelerometers. TDRs can be used to study the foraging behaviour
109 of diving marine predators over several consecutive annual cycles, such as in Adélie
110 penguins (Lescroël et al., 2023). Moreover, the coarser data resolution, compared to
111 accelerometer data, generates smaller datasets which require less analytical and
112 computational power. These advantages are very important when working on long-
113 term species monitoring programmes and when aiming to link individual behaviour to
114 fitness (reproduction and survival), and ultimately, population dynamics.

115 Several TDR-derived time-activity budget models or calibrations of metabolic rate
116 with DLW measurement have been built across marine species to estimate energy
117 expenditure (Chappell et al., 1993b; Chivers et al., 2012). Dive metrics such as
118 bottom phase duration and number of undulations within dives were used as proxies
119 of foraging activity (Bost et al., 2007; Lescroël et al., 2021; Viviant et al., 2014). Yet,
120 validation of such metrics is rare, and recent papers tend to show that these metrics
121 alone do not effectively reflect the foraging activity of marine predators (Allegue et al.,
122 2023; Brisson-Curadeau et al., 2021).

123 We examined this question in Adélie penguins, one of the most abundant Antarctic
124 seabird species and ecosystem sentinel of the Southern Ocean (Barbraud et al.,
125 2020; Forcada and Trathan, 2009). This species mostly forages on two species of
126 krill (*Euphausia superba* and *E. crystallorophias*) (Ratcliffe and Trathan, 2012), and
127 are therefore highly dependent on sea-ice conditions (Kokubun et al., 2021; Michelot
128 et al., 2020). Bottom phase duration and undulations have been extensively used to

129 describe its foraging activity. Yet, the thresholds used to define these two parameters
130 are often different across studies. Bottom phase is sometimes considered spanning
131 from the first to last time vertical velocity was $< 0.25 \text{ m.s}^{-1}$ (Ropert-Coudert et al.,
132 2007), sometimes it is considered to be below the 40% deepest part of a dive
133 (Lescroël et al., 2021), and it sometimes spans from the first to last undulation (Bost
134 et al., 2007). Similarly, calculations of the number of undulations within a dive are
135 derived either from changes in vertical velocity alone or with the latter in addition to
136 different intensity thresholds (Bost et al., 2007; Lescroël et al., 2021; Ropert-Coudert
137 et al., 2001). Creating a simple, validated and objective framework to study its
138 foraging behaviour based on depth data could therefore ease study comparisons.

139 The colony located on île des Pétrés, Antarctica, has been extensively monitored
140 since the 1960's. Since the mid 1990's, TDRs were also regularly deployed, followed
141 by accelerometers since 2016. Hence, only eight years of accelerometry data are
142 currently available, compared to twenty-five for TDR. During the 2018-19 breeding
143 season, breeding Adélie penguins were fitted with loggers recording both
144 accelerometry and TDR data (Hicks et al., 2020). Importantly, DLW measurements
145 were collected from these individuals, allowing the calculation of accurate data on
146 energy expenditures. We take advantage of this diverse ecological data collection to
147 develop a framework allowing estimation of energy balance of Adélie penguins from
148 depth data. We use DLW measurements and TDR data to predict energy expenditure
149 from depth data only. We combine behavioural classification based on accelerometry
150 (Chimienti et al., 2022) and the power of machine learning (Pichler and Hartig, 2023)
151 to estimate foraging activity on solely depth data. We compare our results with other
152 methods classic TDR metrics and accelerometers to answer the following research
153 questions: 1. Can depth data be used to predict energy expenditure of marine

154 predators? and 2. Can machine learning help estimate foraging activity of marine
155 predators from depth data without relying on arbitrary thresholds? 3. Furthermore,
156 since foraging is a costly behaviour, we test whether our framework can reproduce
157 the pattern of DEE increase with time spent foraging.

158 **2. MATERIAL AND METHODS**

159 **2.1. Data collection**

160 The study colony is located on Ile des Pétrels, next to the Dumont D'Urville research
161 station, in Adélie Land (66°40' S; 140°01' E). From the 21st December 2018 to the 11
162 January 2019, 58 breeding Adélie penguins (24 females and 34 males) were tracked
163 and monitored. All individuals were in their chick guarding stage, where parents
164 alternate mostly 1-day trips at sea to forage and feed their chicks (Ainley, 2002).
165 Individuals were captured at their nest when both parents were present. To limit
166 disturbance, we only captured one of the partners for each nest. We performed
167 molecular sexing at CEBC as previously described (Marciau et al., 2023) to confirm
168 the sex of each individual *a posteriori*.

169 This study was approved and authorized by the ethics committee number 084 of the
170 Terres Australes et Antarctiques Françaises (TAAF), Comité d'Environnement
171 Polaire and Conseil National de la Protection de la Nature. All experiments were
172 performed in accordance with the guidelines of these committees.

173

174 **2.2. Logger deployment & Data preparation**

175 Data loggers (Axy-Trek, Technosmart, Italy, 40 x 20 x 8 mm, 14g, less than 0.5 % of
176 individuals mass) recording tri-axial acceleration at 100 Hz and pressure at 1 Hz
177 were deployed on the central back region of breeding Adélie penguins and secured
178 using waterproof adhesive Tesa tape and two Colson plastic cable ties. Deployment
179 duration ranged from 46.53 hours to 78.43 hours with an average of 54.82 ± 1.43
180 hours. Trip duration (from first to last dive) ranged from 12.24 hours to 31.94 hours
181 with an average of 22.60 ± 0.98 hours.

182 Upon recovery, data were downloaded and processed using the R programming
183 language. After calculating depth (± 0.1 m) from pressure (Leroy and Parthiot, 1998),
184 a custom function (see available code) was used to perform the zero-offset
185 correction. Static acceleration was calculated by smoothing each axis over a 1-s
186 period. Then, Dynamic Body Acceleration (DBA) was calculated by subtracting static
187 acceleration from raw acceleration value. Vectorial DBA (VeDBA) was calculated as
188 the square root of the sum of the squares DBA of the three axes.

189 Daily energy expenditure (DEE, kJ/day) was measured using the doubly labelled
190 water technique, as described in Hicks et al. (Hicks et al., 2020). DEE was corrected
191 by the mass of the individual upon equipment to get a mass specific DEE (kJ/g/day).

192

193 **2.3. Behavioural assignment on depth data for energy** 194 **expenditure estimation**

195 For each individual, we calculated the time spent in a given behaviour across logger
196 deployment. Each behaviour was defined based on depth data. An individual was
197 considered diving when it was below 2m, swimming/resting on the water when it was
198 above 1m, and in subsurface or proposing when it was between 1 and 2m (fig. 1).
199 Penguins were considered on land between logger deployment and first dive, last
200 dive and logger recovery, and when they were on the surface for more than 6 hours.
201 In addition to duration, we quantified the overall sum of vertical movement for each
202 phase (except land).

203

204 **2.4. Machine learning approach for foraging detection**

205 In addition to raw depth value, we derived a set of parameters from depth data to
206 feed our machine learning algorithm and describe foraging behaviour. For each dive,
207 we calculated the maximum depth and the dive duration (continuous period below
208 2m). To estimate fine-scale movement, we calculated the vertical velocity as a
209 derivative of depth between time T and T-1 (eqn. 1) and the vertical acceleration as
210 the derivative of velocity between time T and T-1 (eqn. 2, fig. 1) for each data point
211 (1Hz resolution). To estimate broader-scale movement, we calculated the rolling
212 mean and standard deviation of vertical velocity and vertical acceleration over a 5-
213 seconds period.

$$214 \qquad \qquad \qquad \textit{Verticalvelocity}_T = \textit{Depth}_T - \textit{Depth}_{T-1}(1)$$

$$215 \qquad \qquad \qquad \textit{Verticalacceleration}_T = \textit{Verticalvelocity}_T - \textit{Verticalvelocity}_{T-1}(2)$$

216 Using a random forest algorithm (RF), we tried to identify periods of foraging in the
217 diving behaviour of Adélie penguins. As a reference, we used the accelerometry-
218 based behavioural classification from Chimienti *et al.* (Chimienti et al., 2022). As this
219 classification was done at 25 Hz, we summarised it at 1 Hz. To be conservative, we
220 considered 1 Hz data point as foraging when at least half of the corresponding 25 Hz
221 were labelled as foraging (Machado-Gaye et al., 2024), regardless of the proportion.
222 Before running the RF, we performed variable selection to reduce the size of our
223 model. We filtered variables based on correlation factor and variables importance
224 measure (VIM, from “Boruta” R package (Kursa and Rudnicki, 2010)). Whenever two
225 variables were highly correlated (>0.8), the one with the lowest VIM was removed
226 from the RF.

227 Remaining variables were used in a RF built using “tidymodels” (Kuhn and Wickham,
228 2020) and “ranger” (Wright and Ziegler, 2017) R packages. We randomly selected
229 and assigned half of the deployments to train the RF, while the other half was kept to
230 test model performance. Train and test dataset had the same sex-ratio. We trained
231 the RF over 6 variables and parametrised it on different numbers of trees (*i.e.* 50,
232 100, 500, 1000). We also tuned the *mtry* parameter, indicating the number of
233 variables randomly sampled as candidates at each split, between 1 and 6 for each
234 number of trees. Finally, the training dataset was further split into training (75%) and
235 testing (25%) and a five-fold cross validation procedure performed on the final
236 training data. The best model was selected based on two widely used metrics,
237 namely accuracy and Area Under the Receiver Operating Characteristic (ROC)
238 Curve (AUC).

239

240 **2.5. Statistical analysis of energetics**

241 All statistical analyses and data manipulations were performed in R version 4.3.1 (R
242 Core Team, 2023). Unless stated otherwise, means \pm SE are provided. All model
243 assumptions were checked using the `plot_model()` function for the “sjplot” (Lüdecke,
244 2023) R package.

245 To estimate energy expenditure from depth data, we modelled the DLW-derived DEE
246 using linear models with sex, time spent in each behaviour, and sum of vertical
247 movement over each behaviour at the daily level. We compared all combinations
248 using Akaike’s information criterion corrected for small sample size (AICc) and
249 Bayesian information criterion (BIC). To estimate the prediction power of our model,
250 we implemented a bootstrap procedure to limit the effect of our reduced sample size.

251 Over 1000 iterations, the dataset was randomly separated in a train (50%) and test
252 (50%) dataset. After fitting the best model to the train dataset, we compared its
253 depth-derived DEE to the DLW-derived on the test dataset. For each coefficient, we
254 calculated a 95% confidence interval to estimate model stability.

255 To estimate foraging activity from depth data, we modelled at the daily level the
256 accelerometry-derived time spent foraging at-sea T_{foraging} with the RF-derived T_{foraging}
257 , the RF-derived number of prey catching attempts (PCA, *i.e.* continuous foraging
258 period), and two widely-used proxies to quantify foraging intensity, namely bottom
259 duration (*i.e.* time spent in the 20% deepest part of a dive (Bestley et al., 2015; Carter
260 et al., 2017) and number of undulations (*i.e.* change from a negative to positive or
261 positive to negative vertical velocity in the bottom phase (Lescroël et al., 2021)).
262 Again, all model combinations were compared using AICc and BIC.

263 3. RESULTS

264 3.1. Energy expenditure estimation

265 The most parsimonious model was able to reliably predict DLW-estimated DEE
266 (adjusted $R^2 = 0.70$, fig. S1). This model retained only 3 parameters: time spent
267 diving, amount of vertical movement in the sub-surface phase, and sex (eqn. 3, table
268 1). All models within a $\Delta AICc$ of 2 contained both time and movement-based
269 parameters (table 1). In all models, even when it was retained, sex was never
270 significant. In comparison, the most parsimonious model performed significantly
271 better than the best time-activity model ($\Delta AICc = 3.28$, table S1) and the null VEBDA
272 model ($\Delta AICc = 8.15$).

$$\begin{aligned} 273 \quad DEE = & (0.33 \pm 0.04) + (4.21 \times 10^{-2} \pm 6.77 \times 10^{-3})Time_{Dive} + \\ 274 \quad & (2.35 \times 10^{-3} \pm 4.59 \times 10^{-4})Verticalmovement_{Subsurface} + \\ 275 \quad & (-3.81 \times 10^{-2} \pm 2.27 \times 10^{-2})Sex(3) \end{aligned}$$

276 The bootstrap procedure confirmed the robustness of our model to predict DEE from
277 depth data (fig. 2, $\rho = 0.81$ [0.64; 0.91], $R^2 = 0.69$ [0.45; 0.85]) and was coherent with
278 model coefficient calculated on the full dataset.

279

280 3.2. Random forest

281 During model tuning, accuracy and AUC plateaued when $mtry$ reached 3 and $ntrees$
282 1000. With these parameters, the Out-Of-Bar (OOB) error estimated the RF algorithm
283 was 0.03, indicating the good predictive power of our model. In decreasing order of
284 importance, retained variables were the rolling SD of vertical acceleration, the rolling
285 mean of vertical velocity, the depth, the dive duration, the rolling mean of vertical

286 acceleration, and vertical acceleration (fig. S2). Overall accuracy of the model was
287 high, with a balanced accuracy of 0.83, specificity of 0.95 and sensitivity of 0.72.
288 When evaluating the fine scale detection of foraging events, we observed that the
289 model tends to group short consecutive PCA. Nonetheless, the overall foraging
290 duration was very similar to the accelerometry-based reference label and our RF
291 forest algorithm detected foraging periods during the ascend phase of the dives (fig.
292 3).

293

294 **3.3. Foraging activity estimation and comparison with other** 295 **proxies**

296 We investigated if our RF algorithm could predict time spent foraging at-sea and
297 compared it with historical proxies. Our RF efficiently predicted accelerometry-based
298 time spent foraging over a foraging trip from TDR-data ($R^2 = 0.81$, $AICc = 18.22$).
299 This model was significantly better at predicting the reference accelerometry-based
300 time spent foraging than bottom phase duration ($R^2 = 0.51$, $AICc = 40.76$) and
301 number of undulations ($R^2 = 0.32$, $AICc = 48.78$ table 2). Using multiple foraging
302 proxies did not significantly increase the predictive power of our model (fig. 4, table
303 S2). All proxies were predicting time spent foraging better than the null model with
304 trip duration only ($R^2 = 0.04$, $AICc = 57.15$)

305

306 **3.4. At-sea energetics of Adélie penguins**

307 On average, penguins spent 1.84 ± 0.11 hours foraging per trip (0.81 ± 0.05 hours
308 per day). Over that same period, individuals expend on average 0.63 ± 0.02 $\text{kJ}\cdot\text{g}^{-1}$
309 per day, which corresponds to a mean DEE of 2983.01 ± 72.99 kJ. Penguins

310 spending more time foraging per day displayed comparatively higher DEE (fig. 5,
311 table S3, estimate = 0.11 ± 0.04 , $p < 0.01$). For a given foraging duration, females
312 had higher DEE than males (estimate = -0.09 ± 0.03).

313

314 **4. DISCUSSION**

315 We present a novel method to quantify energetics (i.e energy acquisition and
316 expenditure) based on depth data recorded from diving marine predators. We
317 demonstrate the reliability of this method by using foraging trips from 48 Adélie
318 penguins during the chick-rearing stage in the 2018-19 breeding-season.

319 Recordings from depth data provide information on animal movement in just one
320 spatial dimension (y-axis), unlike accelerometry, which covers three spatial
321 dimensions (x, y and z-axis). Furthermore, the temporal resolution of depth data is
322 lower (1 Hz for TDR) compared to that of accelerometers (25 Hz or more). Yet,
323 despite the lower spatial and temporal resolution, our results show that solely based
324 on depth data, the machine learning algorithm RF can be used to identify fine-scale
325 (1 Hz) foraging behaviour (e.g foraging events, prey encounters) with a good
326 accuracy when trained from accelerometer data (accuracy = 0.83).

327 Our RF model was able to predict the foraging pattern detected with the
328 accelerometry. However, the model grouped short prey catching attempts in single
329 foraging bouts, which was expected given the lower resolution of depth data.

330 Therefore, further investigation (e.g. using video cameras for example) is needed to
331 assess what is being caught during these prey catching attempts (Del Caño et al.,
332 2021; Sutton et al., 2020). Historical proxies like bottom duration or number of
333 undulations were solely used to estimate proxies of foraging intensity without

334 knowledge of when foraging was performed (Bost et al., 2007; Lescroël et al., 2021).
335 Moreover, these historical proxies rely on the hypothesis that foraging is occurring
336 mainly, if not totally, during the bottom phase of the dive (Deagle et al., 2008; Falk et
337 al., 2000). Yet, accelerometry (Chimienti et al., 2022), oesophagus sensors (Ropert-
338 Coudert et al., 2000) and video data (Del Caño et al., 2021; Sutton et al., 2020) have
339 shown that penguins also feed during the ascent phase of their dive. By training our
340 RF on foraging detected from accelerometry, our method was able to more precisely
341 identify when feeding is happening using depth data, even during the ascent phase
342 of dives, which was not possible with historical proxies. Moreover, the method
343 presented in this paper presents the advantage of not needing arbitrary thresholds to
344 define states such as bottom-phase or undulations, which could allow its application
345 on other diving marine predators.

346 Overall, our method could likely be applied to other marine predators with TDR and
347 accelerometer data availability to train species-specific RF algorithms. Indeed, the
348 metrics used in this paper to estimate foraging are a simple and objective way of
349 describing movement of diving predators. In addition to outperforming historical
350 proxies like undulations and dive bottom phase duration, using this method would
351 have the advantage to provide a simplified and unbiased comparison between
352 studies. Yet, further investigations are needed to evaluate how our algorithm
353 efficiently detects foraging for different types of prey, as foraging tactics and
354 movement can change depending on the prey (Bowen et al., 2002). Krill is the main
355 prey item of Adélie penguins, but they are also known to forage on fishes or squids
356 (Ratcliffe and Trathan, 2012). Therefore, our dataset is likely to contain foraging of
357 other prey than krill. Hence, our algorithm might also be set to investigate foraging of
358 other penguin species if the metrics derived from TDR data are similar.

359

360

361 Moreover, we found that DEE increased with the proportion of time spent foraging
362 per day. Because foraging is costly for diving marine predators (Jeanniard-du-Dot et
363 al., 2017; Yeates et al., 2007), this correlation supports the idea that our methodology
364 is reliable to estimate the energetics of Adélie penguins, and the benefits of studying
365 energetics as both intake and expenditure rather than focusing on expenditure.
366 Therefore, even if estimated time spent foraging needs further validation, our
367 innovative methodology should improve our ability to study individual energetic trade-
368 offs at large spatial and temporal scales. Here we identified a positive linear
369 relationship between time spent foraging and DEE. Further studies could relate
370 foraging duration to energy intake using mass gain measures and diet energy
371 content estimation to better describe the extent of that relationship. Alternatively,
372 validation of foraging detected through accelerometer using camera logger (Sutton et
373 al., 2020; Watanabe et al., 2019) could link our estimated time spent foraging to
374 energy intake.

375 With a R^2 of 0.70, our low-resolution TDR-based model provides comparable results
376 to other DLW calibrations based on high-resolution accelerometers on marine and
377 terrestrial species like Adélie penguin ($R^2 = 0.75$) (Hicks et al., 2020) or little penguins
378 ($R^2 = 0.78$) (Sutton et al., 2021) or polar bear ($R^2 = 0.70$) (Pagano and Williams,
379 2019). This equation could be applied to the numerous Adélie penguin long-term
380 TDR data collected across Antarctica (Cimino et al., 2023; Lescroël et al., 2023; Riaz
381 et al., 2020), therefore offering a great opportunity to reliably investigate regional
382 variations in energy budgets. In line with what was previously known (Hicks et al.,
383 2020), we showed that assigning different calibration coefficients to different

384 behaviour enhanced predictive power of our model. Our model shows penguins
385 mostly expend their energy while diving and transiting (*i.e.* $\text{Time}_{\text{Dive}}$ and Vertical
386 $\text{movement}_{\text{Sub-surface}}$ eqn.3). Also, despite being retained in the best model, sex was
387 not a significant term and was not present in the second best performing model (Δ
388 $\text{AICc} = 0.42$), making our framework applicable in scenarios where individual sex is
389 not known.

390 It is important to note that during the studied season, there was open water
391 accessible next to the colony, and therefore, penguins did not have to walk long
392 distances to access open water, reducing their energy expenditure (Watanabe *et al.*,
393 2020). Therefore, our calibration might not reflect energy expenditure in areas and
394 years when long walking periods are needed to access open water. Yet, the
395 proposed model could still be relevant when focusing on the at-sea part of the
396 foraging trips. Further investigations would be needed to assess if our model can also
397 be used to estimate at-sea energy expenditure during the other phase of the
398 breeding period, incubation, during which foraging trips are typically longer (10-15
399 days) and diving behaviour is different with shallower and less frequent dives
400 (Chappell *et al.*, 1993a; Lescroël *et al.*, 2023). Yet, in their work Chappell *et al.*
401 (Chappell *et al.*, 1993b) found that the field metabolic rate of Adélie penguins was not
402 significantly different in incubation and chick-rearing.

403 Historically, TDR had been the first type of logger deployed on wild animals
404 (Kooyman, 1965). The described method can easily be applicable to other marine
405 predators, with often longer time-series available for TDR data compared to
406 accelerometers, allowing the study of long-term trends. With environmental changes
407 affecting energy availability (Duncan *et al.*, 2015), these long-term estimations of

408 energetics are crucial to decipher how changing environmental conditions will affect
409 individual life history strategies.

410 In conclusion, we show that lower-resolution TDR data can be used to estimate
411 energetics similarly to accelerometers. Our results demonstrate how the application
412 of machine learning approaches allows researchers to re-analyse datasets and more
413 accurately predict energetics of diving marine predators compared to historical
414 methods. Foraging activity is expected to be related to mass gain (Lescroël et al.,
415 2021). Therefore, with prior knowledge of a species diet, calibrating predicted time
416 spent foraging with mass gain could allow us to refine this simple framework by
417 estimating energy intake directly. Because it's based on the widely used TDR data,
418 this framework could be applied to several long-term marine species monitoring
419 programs. This would allow researchers to study how extrinsic (e.g. environmental
420 variations) and intrinsic (e.g. body condition) variables impact individuals' energetic
421 trade-offs.

422

423 **Acknowledgements:**

424 We thank the Institut Polaire Francais Paul-Emile Victor (IPEV program P1091) for its
425 financial and logistical support.

426

427 **Authors contribution:**

428 BD, AK, YRC and MC conceived the ideas and designed the methodology. OH, DW,
429 CM, FA collected the data. BD analysed the data and wrote the manuscript. All
430 authors contributed critically to the drafts and gave final approval for publication.

431

432 **Conflicts of interests statement:**

433 The authors declare no conflicts of interests

434

435 **Funding:**

436 This project has received funding from the European Union's Horizon 2020 research
437 and innovation programme under the Marie Sklodowska-Curie grant agreement No
438 890284, "Modelling Foraging Fitness in Marine predators (MuFFIN)", awarded to
439 Marianna Chimienti, WWF-UK and PEW foundation. This work is part of a PhD
440 project funded by a grant from the French ministry of higher education and research
441 awarded to Benjamin Dupuis.

442

443 **Data availability:**

444 All code used in this paper are available at <https://github.com/bendps/tdr2nrj>

445 **Diversity and inclusion statement:**

446 All authors were engaged early on with the research and study design to ensure that

447 the diverse sets of perspectives they represent was considered from the onset.

448 Whenever relevant, literature published by scientists from different regions was cited.

449

450 REFERENCES

- 451 Ainley, D., 2002. The Adélie Penguin: Bellwether of Climate Change, in: The Adélie
452 Penguin. Columbia University Press. <https://doi.org/10.7312/ainl12306>
- 453 Allegue, H., Réale, D., Picard, B., Guinet, C., 2023. Track and dive-based movement
454 metrics do not predict the number of prey encountered by a marine predator.
455 *Movement Ecology* 11, 3. <https://doi.org/10.1186/s40462-022-00361-2>
- 456 Barbraud, C., Delord, K., Bost, C.A., Chaigne, A., Marteau, C., Weimerskirch, H.,
457 2020. Population trends of penguins in the French Southern Territories. *Polar*
458 *Biol* 43, 835–850. <https://doi.org/10.1007/s00300-020-02691-6>
- 459 Bestley, S., Jonsen, I.D., Hindell, M.A., Harcourt, R.G., Gales, N.J., 2015. Taking
460 animal tracking to new depths: synthesizing horizontal–vertical movement
461 relationships for four marine predators. *Ecology* 96, 417–427.
462 <https://doi.org/10.1890/14-0469.1>
- 463 Bost, C.A., Handrich, Y., Butler, P.J., Fahlman, A., Halsey, L.G., Woakes, A.J.,
464 Ropert-Coudert, Y., 2007. Changes in dive profiles as an indicator of feeding
465 success in king and Adélie penguins. *Deep Sea Research Part II: Topical*
466 *Studies in Oceanography* 54, 248–255.
467 <https://doi.org/10.1016/j.dsr2.2006.11.007>
- 468 Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., Marshall, G.J., 2002. Prey-
469 dependent foraging tactics and prey profitability in a marine mammal. *Marine*
470 *Ecology Progress Series* 244, 235–245. <https://doi.org/10.3354/meps244235>
- 471 Brisson-Curadeau, É., Handrich, Y., Elliott, K.H., Bost, C.-A., 2021. Accelerometry
472 predicts prey-capture rates in the deep-diving king penguin *Aptenodytes*
473 *patagonicus*. *Mar Biol* 168, 156. <https://doi.org/10.1007/s00227-021-03968-y>
- 474 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a
475 Metabolic Theory of Ecology. *Ecology* 85, 1771–1789.
476 <https://doi.org/10.1890/03-9000>
- 477 Burger, J.R., Hou, C., Brown, J.H., 2019. Toward a metabolic theory of life history.
478 *Proceedings of the National Academy of Sciences* 116, 26653–26661.
479 <https://doi.org/10.1073/pnas.1907702116>
- 480 Byrne, B., Kort, S.R. de, Pedley, S.M., 2022. Leafcutter ants adjust foraging
481 behaviours when exposed to noise disturbance. *PLOS ONE* 17, e0269517.
482 <https://doi.org/10.1371/journal.pone.0269517>
- 483 Carter, M.I.D., Russell, D.J.F., Embling, C.B., Blight, C.J., Thompson, D., Hosegood,
484 P.J., Bennett, K.A., 2017. Intrinsic and extrinsic factors drive ontogeny of
485 early-life at-sea behaviour in a marine top predator. *Sci Rep* 7, 15505.
486 <https://doi.org/10.1038/s41598-017-15859-8>
- 487 Chappell, M.A., Shoemaker, V.H., Janes, D.N., Bucher, T.L., Maloney, S.K., 1993a.
488 Diving Behavior During Foraging in Breeding Adélie Penguins. *Ecology* 74,
489 1204–1215. <https://doi.org/10.2307/1940491>
- 490 Chappell, M.A., Shoemaker, V.H., Janes, D.N., Maloney, S.K., Bucher, T.L., 1993b.
491 Energetics of Foraging in Breeding Adélie Penguins. *Ecology* 74, 2450–2461.
492 <https://doi.org/10.2307/1939596>
- 493 Chevallay, M., Guinet, C., Jeanniard-Du-Dot, T., 2022. Should I stay or should I go?
494 Behavioral adjustments of fur seals related to foraging success. *Behavioral*
495 *Ecology* 33, 634–643. <https://doi.org/10.1093/beheco/arac012>
- 496 Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J., Scott,
497 B.E., 2016. The use of an unsupervised learning approach for characterizing

498 latent behaviors in accelerometer data. *Ecology and Evolution* 6, 727–741.
499 <https://doi.org/10.1002/ece3.1914>

500 Chimienti, M., Kato, A., Hicks, O., Angelier, F., Beaulieu, M., Ouled-Cheikh, J.,
501 Marciau, C., Raclot, T., Tucker, M., Wisniewska, D.M., Chiaradia, A., Ropert-
502 Coudert, Y., 2022. The role of individual variability on the predictive
503 performance of machine learning applied to large bio-logging datasets. *Sci*
504 *Rep* 12, 19737. <https://doi.org/10.1038/s41598-022-22258-1>

505 Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R., Reid, N.,
506 2012. Foraging trip time-activity budgets and reproductive success in the
507 black-legged kittiwake. *Marine Ecology Progress Series* 456, 269–277.
508 <https://doi.org/10.3354/meps09691>

509 Cimino, M.A., Conroy, J.A., Connors, E., Bowman, J., Corso, A., Ducklow, H., Fraser,
510 W., Friedlaender, A., Kim, H.H., Larsen, G.D., Moffat, C., Nichols, R., Pallin,
511 L., Patterson-Fraser, D., Roberts, D., Roberts, M., Steinberg, D.K., Thibodeau,
512 P., Trinh, R., Schofield, O., Stammerjohn, S., 2023. Long-term patterns in
513 ecosystem phenology near Palmer Station, Antarctica, from the perspective of
514 the Adélie penguin. *Ecosphere* 14, e4417. <https://doi.org/10.1002/ecs2.4417>

515 Deagle, B.E., Gales, N.J., Hindell, M.A., 2008. Variability in foraging behaviour of
516 chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to
517 diet. *Marine Ecology Progress Series* 359, 295–309.
518 <https://doi.org/10.3354/meps07307>

519 Del Caño, M., Quintana, F., Yoda, K., Dell’Omo, G., Blanco, G.S., Gómez-Laich, A.,
520 2021. Fine-scale body and head movements allow to determine prey capture
521 events in the Magellanic Penguin (*Spheniscus magellanicus*). *Mar Biol* 168,
522 84. <https://doi.org/10.1007/s00227-021-03892-1>

523 Duncan, C., Chauvenet, A.L.M., Brown, M.E., Petteorelli, N., 2015. Energy availability,
524 spatio-temporal variability and implications for animal ecology. *Diversity*
525 *Distrib.* 21, 290–301. <https://doi.org/10.1111/ddi.12270>

526 Egert-Berg, K., Handel, M., Goldshtein, A., Eitan, O., Borissov, I., Yovel, Y., 2021.
527 Fruit bats adjust their foraging strategies to urban environments to diversify
528 their diet. *BMC Biol* 19, 1–11. <https://doi.org/10.1186/s12915-021-01060-x>

529 English, H.M., Börger, L., Kane, A., Ciuti, S., 2024. Advances in biologging can
530 identify nuanced energetic costs and gains in predators. *Mov Ecol* 12, 1–17.
531 <https://doi.org/10.1186/s40462-024-00448-y>

532 Falk, K., Benvenuti, S., Dall’antonia, L., Kampp, K., Ribolini, A., 2000. Time allocation
533 and foraging behaviour of chick-rearing Brünnich’s Guillemots *Uria lomvia* in
534 high-arctic Greenland. *Ibis* 142, 82–92. <https://doi.org/10.1111/j.1474-919X.2000.tb07687.x>

536 Forcada, J., Trathan, P.N., 2009. Penguin responses to climate change in the
537 Southern Ocean. *Global Change Biology* 15, 1618–1630.
538 <https://doi.org/10.1111/j.1365-2486.2009.01909.x>

539 Froget, G., Butler, P.J., Woakes, A.J., Fahlman, A., Kuntz, G., Le Maho, Y.,
540 Handrich, Y., 2004. Heart rate and energetics of free-ranging king penguins
541 (*Aptenodytes patagonicus*). *J Exp Biol* 207, 3917–3926.
542 <https://doi.org/10.1242/jeb.01232>

543 Gallon, S., Bailleul, F., Charrassin, J.-B., Guinet, C., Bost, C.-A., Handrich, Y.,
544 Hindell, M., 2013. Identifying foraging events in deep diving southern elephant
545 seals, *Mirounga leonina*, using acceleration data loggers. *Deep Sea Research*
546 *Part II: Topical Studies in Oceanography, Fourth International Symposium on*
547 *Bio-logging Science* 88–89, 14–22. <https://doi.org/10.1016/j.dsr2.2012.09.002>

548 Gower, C.N., Garrott, R.A., White, P.J., Watson, F.G.R., Cornish, S.S., Becker, M.S.,
549 2008. Chapter 18 Spatial Responses of Elk to Wolf Predation Risk: Using the
550 Landscape to Balance Multiple Demands, in: Garrott, R.A., White, P.J.,
551 Watson, F.G.R. (Eds.), *Terrestrial Ecology, The Ecology of Large Mammals in*
552 *Central Yellowstone*. Elsevier, pp. 373–399. [https://doi.org/10.1016/S1936-](https://doi.org/10.1016/S1936-7961(08)00218-2)
553 [7961\(08\)00218-2](https://doi.org/10.1016/S1936-7961(08)00218-2)

554 Hazen, E.L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M.G., Savoca, M.S., Scales,
555 K.L., Sydeman, W.J., Bograd, S.J., 2019. Marine top predators as climate and
556 ecosystem sentinels. *Frontiers in Ecology and the Environment* 17, 565–574.
557 <https://doi.org/10.1002/fee.2125>

558 Hicks, O., Kato, A., Angelier, F., Wisniewska, D.M., Hambly, C., Speakman, J.R.,
559 Marciau, C., Ropert-Coudert, Y., 2020. Acceleration predicts energy
560 expenditure in a fat, flightless, diving bird. *Sci Rep* 10, 21493.
561 <https://doi.org/10.1038/s41598-020-78025-7>

562 Jeanniard-du-Dot, T., Guinet, C., Arnould, J.P.Y., Speakman, J.R., Trites, A.W.,
563 2017. Accelerometers can measure total and activity-specific energy
564 expenditures in free-ranging marine mammals only if linked to time-activity
565 budgets. *Functional Ecology* 31, 377–386. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2435.12729)
566 [2435.12729](https://doi.org/10.1111/1365-2435.12729)

567 Kokubun, N., Emmerson, L., McInnes, J., Wienecke, B., Southwell, C., 2021. Sea-ice
568 and density-dependent factors affecting foraging habitat and behaviour of
569 Adélie penguins throughout the breeding season. *Mar Biol* 168, 97.
570 <https://doi.org/10.1007/s00227-021-03899-8>

571 Kokubun, N., Kim, J.-H., Shin, H.-C., Naito, Y., Takahashi, A., 2011. Penguin head
572 movement detected using small accelerometers: a proxy of prey encounter
573 rate. *Journal of Experimental Biology* 214, 3760–3767.
574 <https://doi.org/10.1242/jeb.058263>

575 Kooyman, G.L., 1965. Techniques used in measuring diving capacities of Weddell
576 Seals. *Polar Record* 12, 391–394.
577 <https://doi.org/10.1017/S003224740005484X>

578 Kressler, M.M., Dall, S.R.X., Sherley, R.B., 2023. A framework for studying ecological
579 energy in the contemporary marine environment. *ICES Journal of Marine*
580 *Science fsad082*. <https://doi.org/10.1093/icesjms/fsad082>

581 Kuhn, M., Wickham, H., 2020. Tidy models: a collection of packages for modeling and
582 machine learning using tidyverse principles.

583 Kurs, M.B., Rudnicki, W.R., 2010. Feature Selection with the Boruta Package.
584 *Journal of Statistical Software* 36, 1–13.

585 Leroy, C.C., Parthiot, F., 1998. Depth-pressure relationships in the oceans and seas.
586 *The Journal of the Acoustical Society of America* 103, 1346–1352.
587 <https://doi.org/10.1121/1.421275>

588 Lescroël, A., Schmidt, A., Ainley, D.G., Dugger, K.M., Elrod, M., Jongsomjit, D.,
589 Morandini, V., Winquist, S., Ballard, G., 2023. High-resolution recording of
590 foraging behaviour over multiple annual cycles shows decline in old Adélie
591 penguins' performance. *Proceedings of the Royal Society B: Biological*
592 *Sciences* 290, 20222480. <https://doi.org/10.1098/rspb.2022.2480>

593 Lescroël, A., Schmidt, A., Elrod, M., Ainley, D.G., Ballard, G., 2021. Foraging dive
594 frequency predicts body mass gain in the Adélie penguin. *Sci Rep* 11, 22883.
595 <https://doi.org/10.1038/s41598-021-02451-4>

596 Lüdtke, D., 2023. *sjPlot: Data Visualization for Statistics in Social Science*.

597 Machado-Gaye, A.L., Kato, A., Chimienti, M., Gobel, N., Ropert-Coudert, Y.,
598 Barbosa, A., Soutullo, A., 2024. Using latent behavior analysis to identify key
599 foraging areas for Adélie penguins in a declining colony in West Antarctic
600 Peninsula. *Mar Biol* 171, 69. <https://doi.org/10.1007/s00227-024-04390-w>

601 Marciau, C., Raclot, T., Bestley, S., Barbraud, C., Delord, K., Hindell, M.A., Kato, A.,
602 Parenteau, C., Poupart, T., Ribout, C., Ropert-Coudert, Y., Angelier, F., 2023.
603 Body condition and corticosterone stress response, as markers to investigate
604 effects of human activities on Adélie penguins (*Pygoscelis adeliae*). *Front.*
605 *Ecol. Evol.* 11. <https://doi.org/10.3389/fevo.2023.1099028>

606 Michelot, C., Kato, A., Raclot, T., Shiomi, K., Goulet, P., Bustamante, P., Ropert-
607 Coudert, Y., 2020. Sea-ice edge is more important than closer open water
608 access for foraging Adélie penguins: evidence from two colonies. *Mar. Ecol.*
609 *Prog. Ser.* 640, 215–230. <https://doi.org/10.3354/meps13289>

610 Mogensen, S., Post, J.R., 2012. Energy allocation strategy modifies growth–survival
611 trade-offs in juvenile fish across ecological and environmental gradients.
612 *Oecologia* 168, 923–933. <https://doi.org/10.1007/s00442-011-2164-0>

613 Morano, S., Stewart, K.M., Sedinger, J.S., Nicolai, C.A., Vavra, M., 2013. Life-history
614 strategies of North American elk: trade-offs associated with reproduction and
615 survival. *Journal of Mammalogy* 94, 162–172. [https://doi.org/10.1644/12-](https://doi.org/10.1644/12-MAMM-A-074.1)
616 [MAMM-A-074.1](https://doi.org/10.1644/12-MAMM-A-074.1)

617 Nagy, K.A., Girard, I.A., Brown, T.K., 1999. ENERGETICS OF FREE-RANGING
618 MAMMALS, REPTILES, AND BIRDS. *Annual Review of Nutrition* 19, 247–
619 277. <https://doi.org/10.1146/annurev.nutr.19.1.247>

620 Noakes, M.J., Smit, B., Wolf, B.O., McKechnie, A.E., 2013. Thermoregulation in
621 African Green Pigeons (*Treron calvus*) and a re-analysis of insular effects on
622 basal metabolic rate and heterothermy in columbid birds. *J Comp Physiol B*
623 183, 969–982. <https://doi.org/10.1007/s00360-013-0763-2>

624 Pagano, A.M., Williams, T.M., 2019. Estimating the energy expenditure of free-
625 ranging polar bears using tri-axial accelerometers: A validation with doubly
626 labeled water. *Ecology and Evolution* 9, 4210–4219.
627 <https://doi.org/10.1002/ece3.5053>

628 Pichler, M., Hartig, F., 2023. Machine learning and deep learning—A review for
629 ecologists. *Methods in Ecology and Evolution* 14, 994–1016.
630 <https://doi.org/10.1111/2041-210X.14061>

631 Pontzer, H., McGrosky, A., 2022. Balancing growth, reproduction, maintenance, and
632 activity in evolved energy economies. *Current Biology* 32, R709–R719.
633 <https://doi.org/10.1016/j.cub.2022.05.018>

634 R Core Team, 2023. R: A Language and Environment for Statistical Computing. R
635 Foundation for Statistical Computing, Vienna, Austria.

636 Ratcliffe, N., Trathan, P., 2012. A review of the diet and at-sea distribution of
637 penguins breeding within the CAMLR Convention Area. *CCAMLR Science* 19,
638 75–114.

639 Riaz, J., Bestley, S., Wotherspoon, S., Freyer, J., Emmerson, L., 2020. From trips to
640 bouts to dives: temporal patterns in the diving behaviour of chick-rearing
641 Adélie penguins, East Antarctica. *Marine Ecology Progress Series* 654, 177–
642 194. <https://doi.org/10.3354/meps13519>

643 Ropert-Coudert, Y., Baudat, J., Kurita, M., Bost, C.-A., Kato, A., Le Maho, Y., Naito,
644 Y., 2000. Validation of oesophagus temperature recording for detection of prey
645 ingestion on captive Adélie penguins (*Pygoscelis adeliae*). *Marine Biology*
646 137, 1105–1110. <https://doi.org/10.1007/s002270000414>

647 Ropert-Coudert, Y., Beaulieu, M., Hanuise, N., Kato, A., 2009. Diving into the world
648 of biologging. *Endangered Species Research* 10, 21–27.
649 <https://doi.org/10.3354/esr00188>

650 Ropert-Coudert, Y., Kato, A., Baudat, J., Bost, C.-A., Le Maho, Y., Naito, Y., 2001.
651 Feeding strategies of free-ranging Adélie penguins *Pygoscelis adeliae*
652 analysed by multiple data recording. *Polar Biology* 24, 460–466.
653 <https://doi.org/10.1007/s003000100234>

654 Ropert-Coudert, Y., Wilson, R.P., Yoda, K., Kato, A., 2007. Assessing performance
655 constraints in penguins with externally-attached devices. *Marine Ecology*
656 *Progress Series* 333, 281–289. <https://doi.org/10.3354/meps333281>

657 Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K.,
658 Hiraldo, F., 2008. Top Predators as Conservation Tools: Ecological Rationale,
659 Assumptions, and Efficacy. *Annu. Rev. Ecol. Evol. Syst.* 39, 1–19.
660 <https://doi.org/10.1146/annurev.ecolsys.39.110707.173545>

661 Steinhart, G.B., Sandrene, M.E., Weaver, S., Stein, R.A., Marschall, E.A., 2005.
662 Increased parental care cost for nest-guarding fish in a lake with
663 hyperabundant nest predators. *Behavioral Ecology* 16, 427–434.
664 <https://doi.org/10.1093/beheco/ari006>

665 Sutton, G., Pichegru, L., Botha, J.A., Kouzani, A.Z., Adams, S., Bost, C.A., Arnould,
666 J.P.Y., 2020. Multi-predator assemblages, dive type, bathymetry and sex
667 influence foraging success and efficiency in African penguins. *PeerJ* 8, e9380.
668 <https://doi.org/10.7717/peerj.9380>

669 Sutton, G.J., Botha, J.A., Speakman, J.R., Arnould, J.P.Y., 2021. Validating
670 accelerometry-derived proxies of energy expenditure using the doubly labelled
671 water method in the smallest penguin species. *Biol Open* 10, bio055475.
672 <https://doi.org/10.1242/bio.055475>

673 Sydeman, W.J., Poloczanska, E., Reed, T.E., Thompson, S.A., 2015. Climate
674 change and marine vertebrates. *Science* 350, 772–777.
675 <https://doi.org/10.1126/science.aac9874>

676 Viviant, M., Monestiez, P., Guinet, C., 2014. Can We Predict Foraging Success in a
677 Marine Predator from Dive Patterns Only? Validation with Prey Capture
678 Attempt Data. *PLOS ONE* 9, e88503.
679 <https://doi.org/10.1371/journal.pone.0088503>

680 Watanabe, Y.Y., Ito, K., Kokubun, N., Takahashi, A., 2020. Foraging behavior links
681 sea ice to breeding success in Antarctic penguins. *Science Advances* 6,
682 eaba4828. <https://doi.org/10.1126/sciadv.aba4828>

683 Watanabe, Y.Y., Payne, N.L., Semmens, J.M., Fox, A., Huveneers, C., 2019. Hunting
684 behaviour of white sharks recorded by animal-borne accelerometers and
685 cameras. *Marine Ecology Progress Series* 621, 221–227.
686 <https://doi.org/10.3354/meps12981>

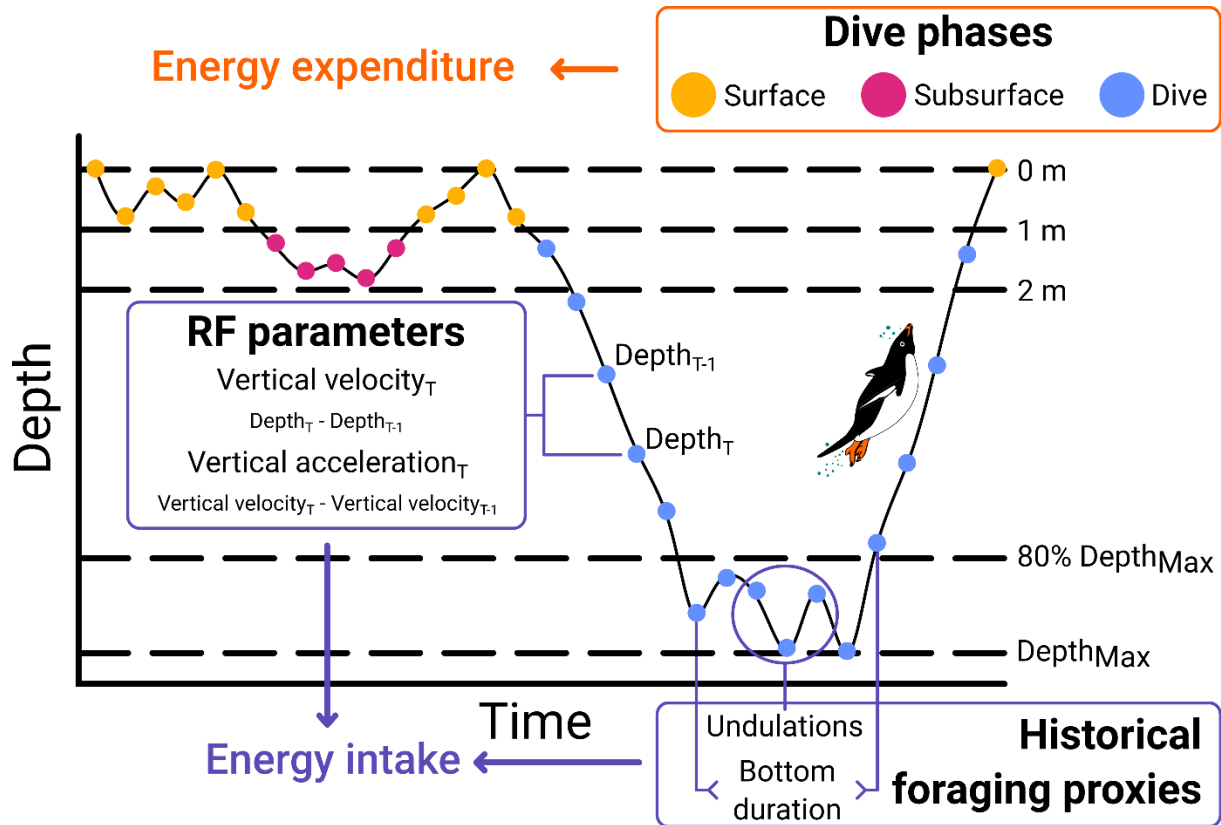
687 Wilson, R.P., Börger, L., Holton, M.D., Scantlebury, D.M., Gómez-Laich, A.,
688 Quintana, F., Rosell, F., Graf, P.M., Williams, H., Gunner, R., Hopkins, L.,
689 Marks, N., Geraldi, N.R., Duarte, C.M., Scott, R., Strano, M.S., Robotka, H.,
690 Eizaguirre, C., Fahlman, A., Shepard, E.L.C., 2020. Estimates for energy
691 expenditure in free-living animals using acceleration proxies: A reappraisal.
692 *Journal of Animal Ecology* 89, 161–172. <https://doi.org/10.1111/1365-2656.13040>

694 Wright, M.N., Ziegler, A., 2017. ranger: A Fast Implementation of Random Forests for
695 High Dimensional Data in C++ and R. *Journal of Statistical Software* 77, 1–17.
696 <https://doi.org/10.18637/jss.v077.i01>

697 Yeates, L.C., Williams, T.M., Fink, T.L., 2007. Diving and foraging energetics of the
698 smallest marine mammal, the sea otter (*Enhydra lutris*). *Journal of*
699 *Experimental Biology* 210, 1960–1970. <https://doi.org/10.1242/jeb.02767>
700

701 FIGURES

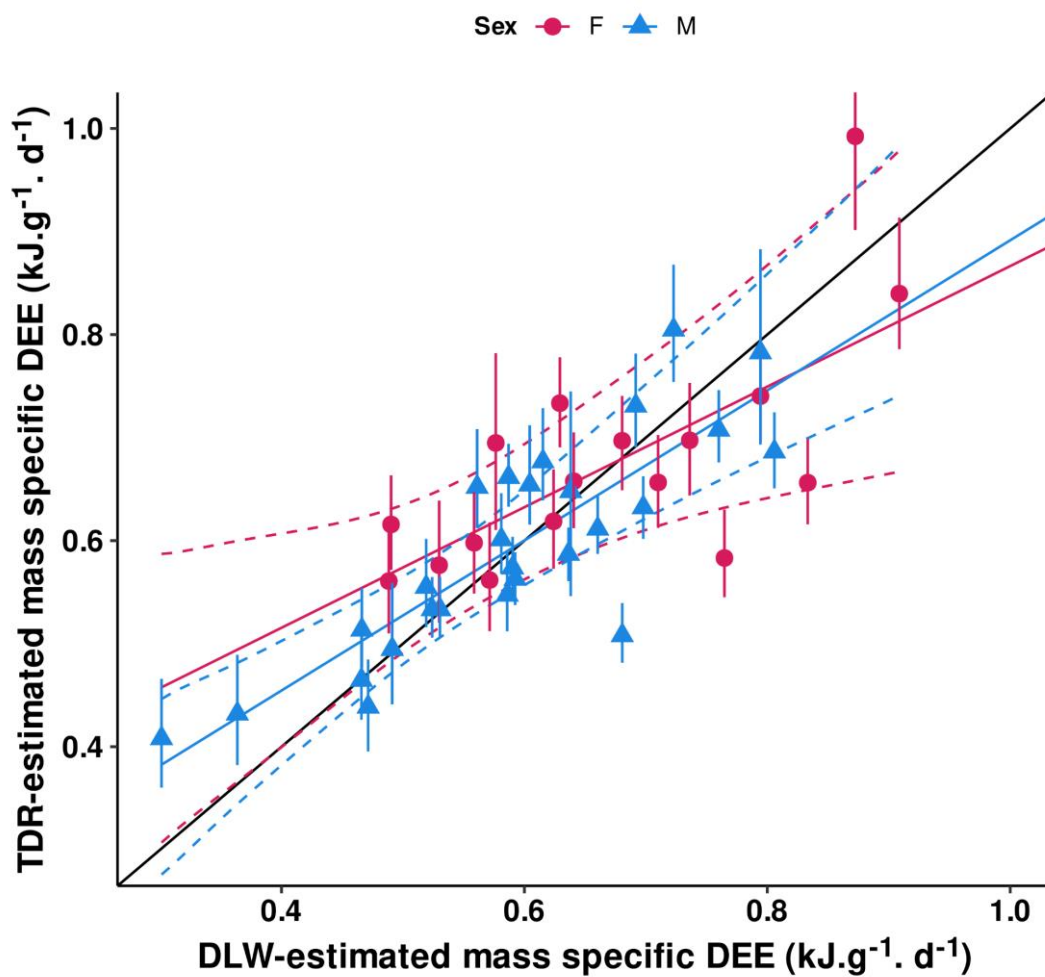
702 **Figure 1.** Conceptual visualization of the depth-derived parameters used to estimate
703 energy balance of Adélie penguins.



704

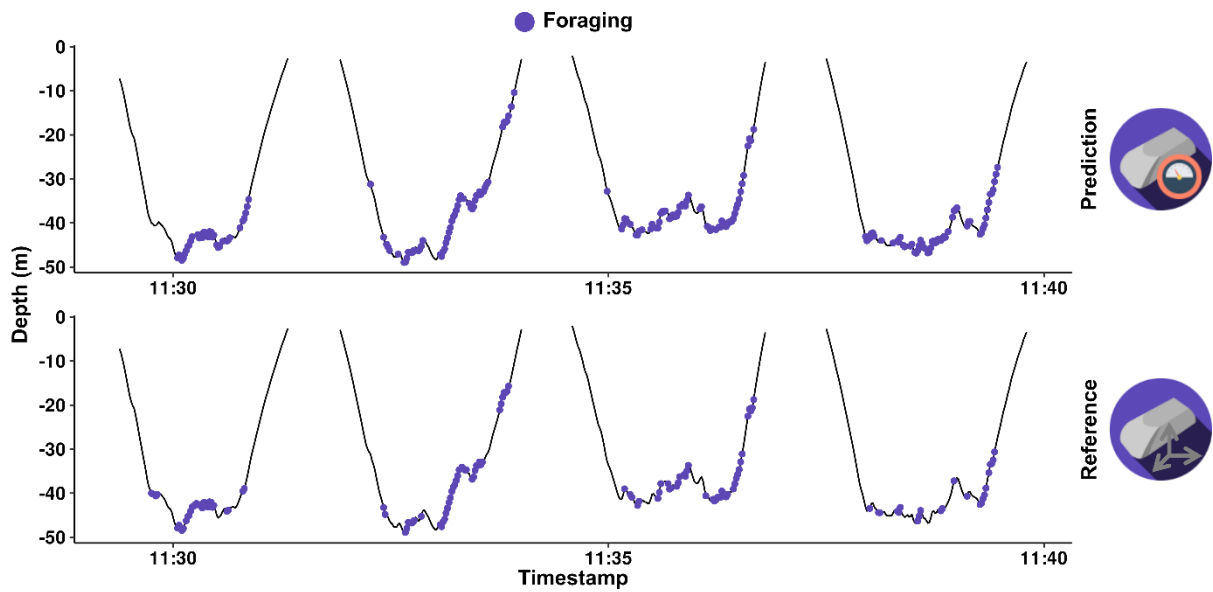
705

706 **Figure 2.** Relation between TDR and DLW-estimated DEE. Dashed lines and error
707 bars represent 95% confidence intervals. The black line represents the $y = x$ slope.



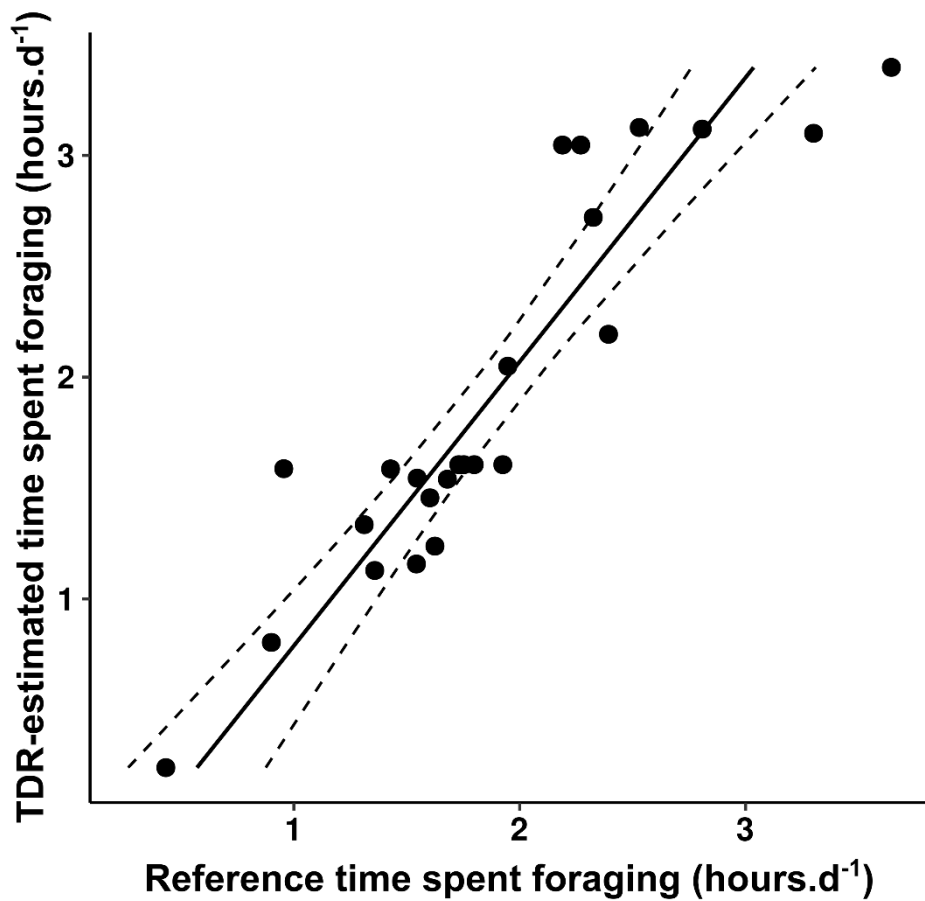
708

709 **Figure 3.** Dive profile of Adélie penguin. A. With the RF algorithm based on depth
710 data. B. With the reference accelerometry-based classification. Purple dots represent
711 foraging.



712

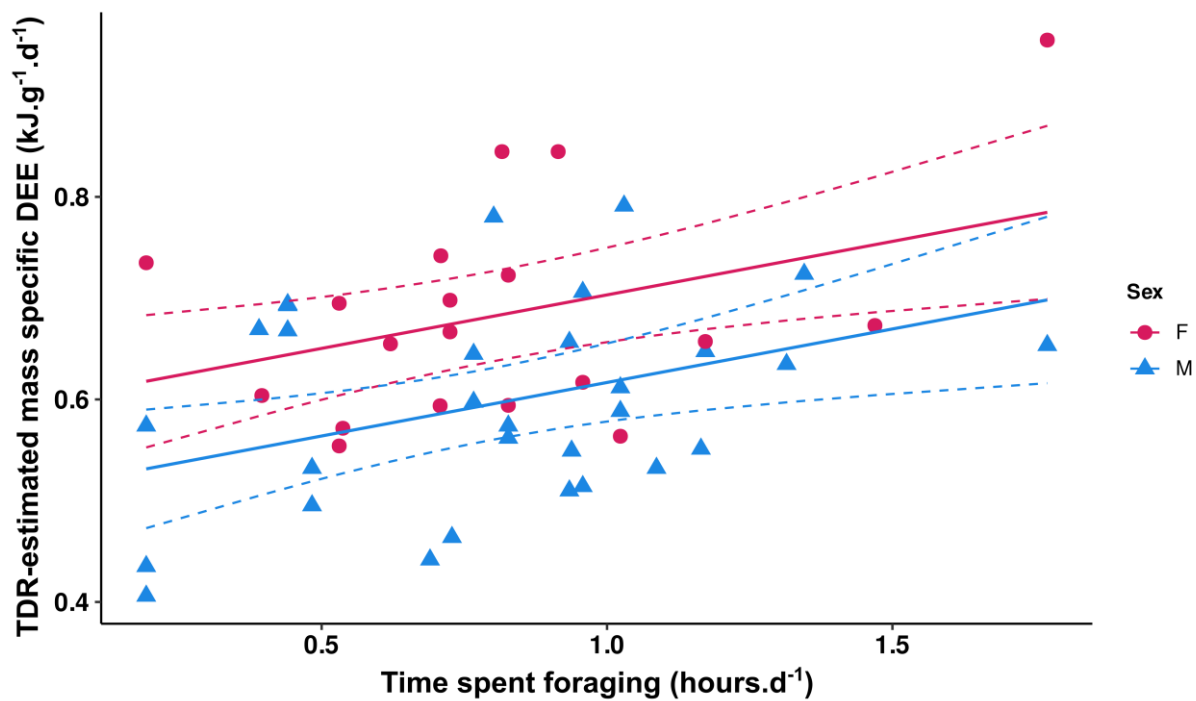
713 **Figure 4.** Output from the most parsimonious model to predict time spent foraging
714 per day at sea. Reference time spent foraging was calculated from high-resolution tri-
715 axial accelerometry data. Dashed lines represent the 95% confidence interval around
716 the regression.



717

718 **Figure 5.** DEE increases with time spent foraging per day over the deployment.

719 Dashed lines represent the 95% confidence interval around the regression.



720

721

722 **Table 1.** Model selection for DLW-derived DEE model. Only models within $\Delta AICc$ of
 723 2 are displayed, as well as the best time-activity model (*), and a null model (**).

724

Formula	Rank	AICc	BIC	$\Delta AICc$	Weight	Adj. R ²
DEE ~ T _{Dive} + Vertical	4.00	-	-	0.00	0.41	0.70
Movement _{Sub-surface} + Sex		100.0	92.6			
		0	8			
DEE ~ T _{Dive} + Vertical	3.00	-	-	0.42	0.33	0.68
Movement _{Sub-surface}		99.58	93.4			
			7			
DEE ~ T _{Dive} + T _{Sub-surface} +	5.00	-	-	1.64	0.18	0.70
Vertical Movement _{Sub-}		98.36	89.9			
surface + Sex			3			
* DEE ~ T _{Dive} + T _{Sub-surface}	3.00	-	-	3.28	0.08	0.66
		96.72	90.6			
			1			
** DEE ~ Mean _{VeDBA}	2.00	-	-	8.15	0.01	0.61
		91.85	87.1			
			0			

725

726 **Table 2.** Model selection for predicting Accelerometry based time spent foraging.
 727 Only models within $\Delta AICc$ of 2 are displayed, as well as three null models, with only
 728 bottom phase duration (*), number of undulations (**), and trip duration (***)).

729

Formula	Ran k	AIC c	BIC	$\Delta AICc$	weig ht	adj.r.sqrd
RefTime spent foraging ~	2.00	18.2	20.5	0.00	0.34	0.81
PredTime spent foraging		2	6			
RefTime spent foraging ~	3.00	18.3	20.9	0.09	0.33	0.82
PredTime spent foraging + TimeBottom phase		1	1			
* RefTime spent foraging ~ TimeBottom phase	2.00	40.7	43.1	22.54	0.00	0.51
** RefTime spent foraging ~ NUndulations	2.00	48.7	51.1	30.56	0.00	0.32
*** RefTime spent foraging ~ Trip duration	2.00	57.1	59.4	38.93	0.00	0.04

730