

1 **Body temperature rebounds on sea ice and is elevated by mercury contamination in a keystone**  
2 **predator**

3  
4 **Melissa L. Grunst<sup>a</sup>, Andrea S. Grunst<sup>a</sup>, David Grémillet<sup>b,c</sup>, Akiko Sato<sup>d</sup>, Sophie Gentès<sup>a</sup>, Jérôme**  
5 **Fort<sup>a</sup>**

6  
7 <sup>a</sup>Littoral, Environnement et Sociétés (LIENSs), UMR 7266 CNRS-La Rochelle Université, 2 Rue Olympe  
8 de Gouges, FR-17000 La Rochelle, France

9 <sup>b</sup>CEFE, UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE;  
10 Montpellier, France

11 <sup>c</sup>Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa

12 <sup>d</sup>Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 CNRS-La Rochelle Université, 79360  
13 Villiers-en-Bois, France

14  
15 **Abstract** Despite overall stability, plasticity in endothermic body temperature ( $T_b$ ) occurs, which may  
16 facilitate maintenance of crucial activities in the face of climate change-related environmental variations.  
17 However, this plasticity may be limited by physiological or energetic constraints, which are potentially  
18 exacerbated by other environmental stressors. For instance, chemical contamination may elevate energetic  
19 costs and have endocrine disrupting effects that undermine thermoregulation. We leveraged advanced  
20 biologging techniques to elucidate how  $T_b$  varies with different behavioral states and environmental  
21 conditions in a keystone Arctic seabird, the little auk (*Alle alle*). We additionally evaluated whether  
22 mercury (Hg) contamination independently affected  $T_b$ , or limited or increased state-dependent changes  
23 in  $T_b$ .  $T_b$  was highest and relatively invariable when birds were at the colony, and rebounded when birds  
24 were resting on sea ice, following declines while foraging (diving) in polar waters. These results suggest  
25 that the colony and sea ice function as thermal refuges for little auks. In addition,  $T_b$  increased with  
26 ambient temperature and relative humidity across behavioral states, and increased with wind speed when

27 birds were flying. Little auks with higher Hg levels had higher, less variable,  $T_b$  across behaviors and  
28 environmental contexts, perhaps reflecting increased metabolic rates linked to detoxification costs.  
29 Results provide evidence for environment- and contaminant-related effects on  $T_b$ , but not interactive  
30 effects between the two, and suggest that loss of sea ice and increased environmental contamination under  
31 global change may have serious implications for  $T_b$  regulation and energy balance.

32 **Keywords:** Body temperature; behavior; plasticity; environmental variation; climate change;  
33 ecotoxicology; mercury; biologging

34

### 35 **Introduction**

36 Endothermic animals are characterized by the ability to tightly regulate body temperature ( $T_b$ ) via  
37 endogenous heat production (McNab 2002). This capacity is potentiated by a high metabolic rate, and  
38 allows endotherms to occupy a breadth of thermal niches, achieve a degree of thermal independence from  
39 environmental temperatures (Khaliq et al. 2014), and sustain impressive levels of activity driven by high  
40 muscular power output (Crompton et al. 1978; Hedrick and Hillman 2016). However, tightly regulating  
41  $T_b$  via thermoregulation also has energetic costs. Consequently, many endothermic species allow adaptive  
42 fluctuations  $T_b$  to minimize thermoregulatory costs and maximize energy balance (Angilletta et al. 2010;  
43 McKechnie and Wolf 2019). Fluctuations in  $T_b$  may reflect weather conditions that modify the thermal  
44 gradient between the body and the environment and the costs of thermoregulation. For instance, small,  
45 overwintering songbirds often allow reductions in  $T_b$  during periods of inactivity, which lowers the  
46 temperature differential between the body and environment, hence reducing heat loss and conserving  
47 energy (McKechnie and Lovegrove 2002; Douglas et al. 2017; Stager et al. 2020). Similarly, animals  
48 facing very hot ambient environmental conditions can allow  $T_b$  to rise, thus reducing thermoregulatory  
49 costs and conserving water (Gerson et al. 2019a; McKechnie and Wolf 2019; Cooper et al. 2020). In the  
50 context of global change, organisms may increasingly face challenging thermal environments, and  
51 adaptive phenotypic plasticity in  $T_b$  could be an important energy-saving mechanism.

52 In addition, endothermic  $T_b$  fluctuates not only with external environmental conditions, but also with  
53 activity. Although heat dissipation mechanisms act to maintain  $T_b$  within a safe range,  $T_b$  often increases  
54 as a result of heat production during intense activities, such as flying (Aulie 1971; Torre-Bueno 19776;  
55 Tapper et al. 2020). However, when temperatures drop below the thermal neutral zone, heat generated by  
56 energy-intensive activities may offset energetic costs of thermoregulation, in which case minimal changes  
57 in  $T_b$  with activity may be observed (Bruinzeel and Piersma 2008; Humphries and Careau 2011; Careau  
58 and Garland 2012). Animals adapted to harness activity to neutralize thermoregulatory costs may suffer  
59 under climate change scenarios of warming temperatures because heat generated by activity no longer  
60 balances thermoregulatory costs, but rather, potentially leads to thermal stress. Consequently, animals  
61 may be forced to reduce activities that fulfill essential ecological and social functions, with non-trivial  
62 effects on fitness (Tapper et al. 2020). On the other hand, as an energy conservation mechanism, animals  
63 may allow  $T_b$  to fall during long periods of inactivity, especially when ambient temperatures are low  
64 (Brodin et al. 2017). Thus, elucidating how climate change-linked increases in environmental temperature  
65 will affect endothermic energy balance depends on understanding how  $T_b$  is regulated according to both  
66 environmental conditions and activity patterns. However, it is challenging to simultaneously measure  
67 variation in  $T_b$ , activity, and environmental parameters through time in the wild. As a result,  
68 comprehensive studies of dynamic  $T_b$  regulation in free-living animals remain scarce, limiting our ability  
69 to predict responses to climate change.

70 Furthermore, organisms do not face the energetic challenges of climate change in isolation, but in  
71 combination with other anthropogenic disturbance factors, such as exposure to chemical contaminants  
72 (Jennsen 2006). Chemical contaminants, such as mercury (Hg), have the potential to disrupt adaptive  $T_b$   
73 regulation in endotherms via a number of mechanisms. For instance, Hg may undermine effective  
74 thermoregulation via endocrine disrupting effects (Rice et al. 2014). Notably, Hg has been shown to  
75 interfere with the production of thyroid hormones, which play a central role in thermoregulation (Wada et  
76 al. 2009). In addition, Hg could affect the adaptive thermal set point by elevating detoxification costs and  
77 resting metabolic rate (Calow 1991), which could be associated with higher  $T_b$ . Although little data

78 specific to Hg is available, both hypo- and hyperthermic responses have been observed in response to  
79 chemical contamination, with hypothermic responses proposed to reflect an adaptive response linked to  
80 declines in chemical toxicity at lower  $T_b$  (Leon 2008; Noyes et al. 2009).

81 In this study, we used a suite of advanced techniques to gain insight into the potential effects of  
82 climate change and chemical contamination (i.e. Hg) levels on  $T_b$  regulation and energetic costs in a  
83 keystone Arctic seabird, the little auk (or dovekie, *Alle alle*). In the Arctic, Hg is an especially prevalent  
84 contaminant that reaches remote polar regions via a repeated process of condensation and evaporation and  
85 bioaccumulates in marine food chains (Morel et al. 1998; Albert et al. 2019; AMAP 2021). Dynamics of  
86 Hg exposure in Arctic animals is being influenced by climate changes. For instance, increases in Hg  
87 exposure may result via release from permafrost and expansion of the low oxygen subsurface zone, in  
88 which inorganic Hg in the ocean is converted to highly toxic methylmercury (Jonsson et al. 2022). We  
89 combined the use of internal  $T_b$  loggers, which recorded abdominal temperature as a proxy of  $T_b$ ,  
90 miniaturized accelerometers that record dynamic body acceleration, allowing classification of activity  
91 patterns, and weather station data to gain insight into patterns of weather- and activity-specific  $T_b$   
92 regulation. In addition, we obtained blood samples to assess total-Hg concentrations in the red blood cells  
93 as a means of assessing whether Hg contamination could affect that ability to maintain stable  $T_b$ .

94 We generated a suite of general and specific predictions based on our knowledge of the behavior,  
95 morphology and energetics of our study species. In general, we predicted that environmental conditions  
96 and activity would interact to affect mean levels and variation in core  $T_b$ . More specifically, little auks  
97 have a morphology that compromises adaptation for diving and flying. This morphology is characterized  
98 by a high wing loading, which results in extremely high energetic costs of flight (Fort et al. 2009; Ste-  
99 Marie et al. 2022). Thus, we predicted that  $T_b$  would increase when birds were flying relative to when  
100 birds were at rest at the colony, on sea ice, or water surface, and that this increase would be magnified  
101 under conditions that reduce heat exchange between the body and environment (i.e. higher temperature,  
102 lower wind speed and relative humidity), which could ultimately limit activity under climate change  
103 scenarios. In contrast, endothermic animals diving into cold polar waters face a significant thermal

104 challenge due to the high thermal conductance of water (Grémillet et al. 2015; Favilla and Costa 2020).  
105 As a result, diving animals often allow  $T_b$  to fall below normothermic levels, which may facilitate aerobic  
106 dive capacity and limit energetic costs of heat loss to the environment (Niizuma et al. 2007; Favilla and  
107 Costa 2020). Thus, we predicted that  $T_b$  would decline over the course of foraging episodes, and would  
108 subsequently increase when birds were resting on sea ice. We also recognized the potential that regional  
109 heterothermy, that is, variation in peripheral temperatures, especially in the appendages, might buffer  
110 changes in core  $T_b$  during diving, resulting in relative stability (Niizuma et al. 2007; Ponganis et al. 2003).  
111 In general, we also predicted that variation in  $T_b$  might increase in the context of thermal challenge, which  
112 in the Arctic is most commonly experienced in the context of cold stress (this might be especially relevant  
113 during resting periods at the colony, on sea ice, or on the water), but which could also involve heat stress,  
114 especially during energetically-demanding activities (i.e. flight). Finally, we predicted that higher blood  
115 Hg levels might affect the adaptive thermal set point and thermoregulatory capacity. Thus, higher Hg  
116 levels could be linked to either higher mean  $T_b$ , perhaps reflecting increased metabolic rates to support  
117 detoxification costs, or lower  $T_b$ , perhaps reflecting suppression of thyroid hormones (Chastel et al. 2022).  
118 In addition, elevated blood Hg could be linked to greater variation in  $T_b$ , especially in the context of  
119 thermal stress.

120

## 121 **Methodology**

122 **Study system:** We studied a breeding population of little auks situated at Ukaleqarteq (Kap Höegh), East  
123 Greenland (70°44'N, 21°35'W). This population has been the subject of intensive research since 2005.  
124 Little auks nest in rock crevasses and can be captured and recaptured at or near the nest site, facilitating  
125 fitting and retrieval of accelerometers and deployment of  $T_b$  loggers. Hg levels in little auks at  
126 Ukaleqarteq now exceed toxicological thresholds and evidence suggests negative effects of Hg on  
127 reproduction (Fort et al. 2014; Carravieri et al. *unpublished*), energetics (Grunst et al. *unpublished*) and  
128 adult body condition (Amélineau et al. 2018).

129

130 **Deployment of  $T_b$  loggers and accelerometers:** During July 2020, 8 individuals were simultaneous fitted  
131 with  $T_b$  loggers (BodyCap Anipill Core Body Temperature Ingestible Tablet; BMedical;  $\pm 1^\circ\text{C}$ ), a  
132 telemetric system for gastrointestinal temperature recording, and miniaturized accelerometers (Axy 4,  
133 Technosmart, 3g), to record dynamic body acceleration and surface temperature. Upon capture, focal  
134 birds ingested  $T_b$  loggers which recorded abdominal temperature (a proxy for  $T_b$ ) every minute for periods  
135 of 24h. We then remotely downloaded the data from  $T_b$  loggers via telemetry when the bird was within  $\sim 1$   
136 m of the device. Accelerometers were attached to the breast of the bird at the level of the sternum and  
137 positioned centrally using Tesa<sup>®</sup> tape adhered to the feathers. We marked birds with color rings to  
138 facilitate identification and recapture within  $\sim 4$  days, upon which we retrieved the accelerometer.  
139 Deployment dates all fell within 9 days during the mid-late chick rearing phase [range July 22-30]. A  
140 weather station erected at the study site documents variation in ambient weather conditions at a frequency  
141 of every 1 minute, including temperature, relative humidity and wind speed.

142  
143 **Analysis of accelerometry and  $T_b$  data:** Accelerometers recorded data at a frequency of 50 Hz (50  
144 readings per second). We used Igor Pro 8.04 (64-bit; WaveMetrics) to classify data on triaxial  
145 acceleration into different behavioral states (see details in Grunst et al. *In Review*). In brief, to identify the  
146 time birds spent engaged in different behavioral states through time, we used k-clustering analysis applied  
147 to acceleration axes, followed by application of a custom-written script, which utilized both the output  
148 from the clustering analysis and surface temperature data. The behavior identified were: flying, diving, on  
149 the water surface, on ice, and at the colony. We proceeded to determine whether time spent on the water  
150 surface was part of an active foraging bout (i.e. an inter-dive interval), or represented time spent resting  
151 on the water surface. To this end, we determined the dive bout ending criterion, using R package  
152 diveMove (Luque 2007), which applies the methods of Sibley et al. (1990) and Mori et al. (2001) for the  
153 identification of behavioral bouts. We used the standard method of classification, based on the absolute  
154 duration of the behavioral bouts (i.e. the inter-dive intervals), rather than the sequential difference

155 method. The bout ending criteria derived was 307.1 seconds. Consequentially, we ended diving bouts if  
156 the length of time spent on the water surface exceeded this value, and classified these intervals as time  
157 spent resting on the water. Time spent resting on the water additionally encompassed intervals of time on  
158 the water that were not between dives. We combined time engaged in diving and inter-dive intervals into  
159 a single behavioral category, representing active foraging. Thus, our final behavioral categories were:  
160 actively foraging (also referred to hereafter as “diving”), flying, at the colony, resting on sea ice, and  
161 resting on the water surface. For each  $T_b$  measurement, we determined which behavioral state the bird  
162 was in at that time by aligning time stamps from the  $T_b$  and behavioral (accelerometer) data in Microsoft  
163 Excel 16.16.27.

164

165 **Mercury contamination: sampling and analysis:** We obtained small ~0.2-0.5 ml blood samples from  
166 the brachial veins of focal individuals. Blood samples were centrifuged for 10 min. at 3500 rpm to  
167 separate plasma from red blood cells (RBCs), which were stored in 70% ethanol. RBCs were freeze dried  
168 for 48 hrs and homogenized prior to analysis for total Hg concentrations. Samples were analyzed in  
169 duplicate using an advanced Hg analyser spectrophotometer (Altec AMA 254) at the Institute Littoral  
170 Environnement et Sociétés, La Rochelle University (Bustamante et al. 2006). The standard deviation  
171 between duplicates was <10%. We used TORT-3 as a standardized reference material (CRM; Lobster  
172 Hepatopancreas Tort-3; NRC, Canada; [Hg] =  $0.292 \pm 0.022 \mu\text{g g}^{-1}$  dry weight (dw)) and performed a  
173 blank before initiating measurements on samples. The limit of detection for Hg and mean  $\pm$  SD of Tort-3  
174 measurements were  $0.005 \mu\text{g g}^{-1}$  dw and  $0.306 \pm 0.004 \mu\text{g g}^{-1}$  dw, respectively.

175

## 176 **Statistical analysis**

177 We conducted statistical analyses in R 3.6.1 (R Core Team, 2019). We used generalized additive mixed  
178 effect models (GAMMs) in R package mgcv (Wood 2011, 2017) to assess whether the mean  $T_b$  of little  
179 auks varied with behavioral activity classes, environmental conditions, or time of day. For this model, we

180 used each observation of  $T_b$ , while including appropriate random effects and correlation structure to  
181 account for non-independence of observations. Specifically, package `mgcv` allowed us to implement a  
182 correlation structure that accounts for temporal autocorrelation (`corAR1` correlation structure  
183 implemented through package `nlme`; Pinheiro et al. 2019), to include individual ID and behavioral bout  
184 as random effects, and to incorporate a non-linear smooth term (cyclic cubic regression spline; specified  
185 as `bs=cc`) to account for potential variation in  $T_b$  with time of day. We included two-way interactions  
186 between behavioral class and: (1) ambient temperature, (2) relative humidity, (3) wind speed, (4) time  
187 spent engaged in the activity, and (5) Hg concentrations measured in the whole blood. These interactions  
188 test whether the relationship between  $T_b$  and behavior is contingent upon external conditions, the amount  
189 of time elapsed in a certain behavior (e.g. flying), and contamination level. We removed interactions with  
190 p-values  $> 0.050$  from models, followed by elimination of main effects above the same threshold. We  
191 used the `emmeans` function in R package `emmeans` to test pairwise comparisons for interaction terms  
192 (Lenth 2019). Pairwise comparisons for mean differences in  $T_b$  between behavioral states were conducted  
193 using function `emmeans` within package `emmeans`. For this purpose, interactions were first removed from  
194 models to avoid complications with interpretation. In addition, to further explore the interaction that  
195 emerged between behavioral state and time spent engaged in the activity, we calculated change in  $T_b$   
196 ( $\Delta T_b$ ) for each behavioral bout as:  $\Delta T_b = T_{b,end} - T_{b,start}$ ; where  $T_{b,end} = T_b$  at the last time point recorded in  
197 that behavioral state and  $T_{b,start} = T_b$  at the first time point recorded. We then used a linear mixed effects  
198 model in `nlme` to compare  $\Delta T_b$ s across behavioral states, and also included the length of the time interval  
199 in the model. We extracted and plotted predicted values from models using R function `ggpredict` within  
200 the `ggeffects` package (Lüdtke 2018).

201 In addition, we assessed whether between minute variation in  $T_b$  differed between behavioral states by  
202 calculating the absolute value of the difference between subsequent measurements of  $T_b$ , and then  
203 constructing models with the same structure as described for mean  $T_b$ . Values could not be calculated for  
204 time points at the beginning of the behavioral intervals, so these rows were dropped from the analysis.

205



206 **Results**

207 **Effect of behavioral state on mean  $T_b$ :** The mean  $\pm$  SD  $T_b$  of little auks across all observations was  
 208  $41.02 \pm 0.55$  (range: 39.29-43.08).  $T_b$  varied significantly with behavioral state ( $F_4 = 33.26$ ;  $P < 0.001$ ;  
 209 Table 1a). Without interactions in the model,  $T_b$  was highest when birds were at the colony, followed by  
 210 flying, and was lowest when birds were resting on the sea ice.  $T_b$  while birds were diving versus resting  
 211 on the water surface did not significantly differ, and was intermediate to  $T_b$  while flying and on the ice.  
 212 Pair-wise comparisons indicated significant differences in  $T_b$  in these states, with the exception of  
 213 between diving and resting on the water (Table 1b). Figure 1 shows a representative trace of  $T_b$  variation  
 214 through time for one focal individual. See Fig. S1-S7 for equivalent traces for the other 7 birds.

215

216 **Table 1.** Differences in mean  $T_b$  of little auks in the five behavioral states: (a) estimated marginal (EM)  
 217 means from the best-fitting GAMM with interactions removed (df = 16391), (b) pairwise contrasts  
 218 between behavioral states.

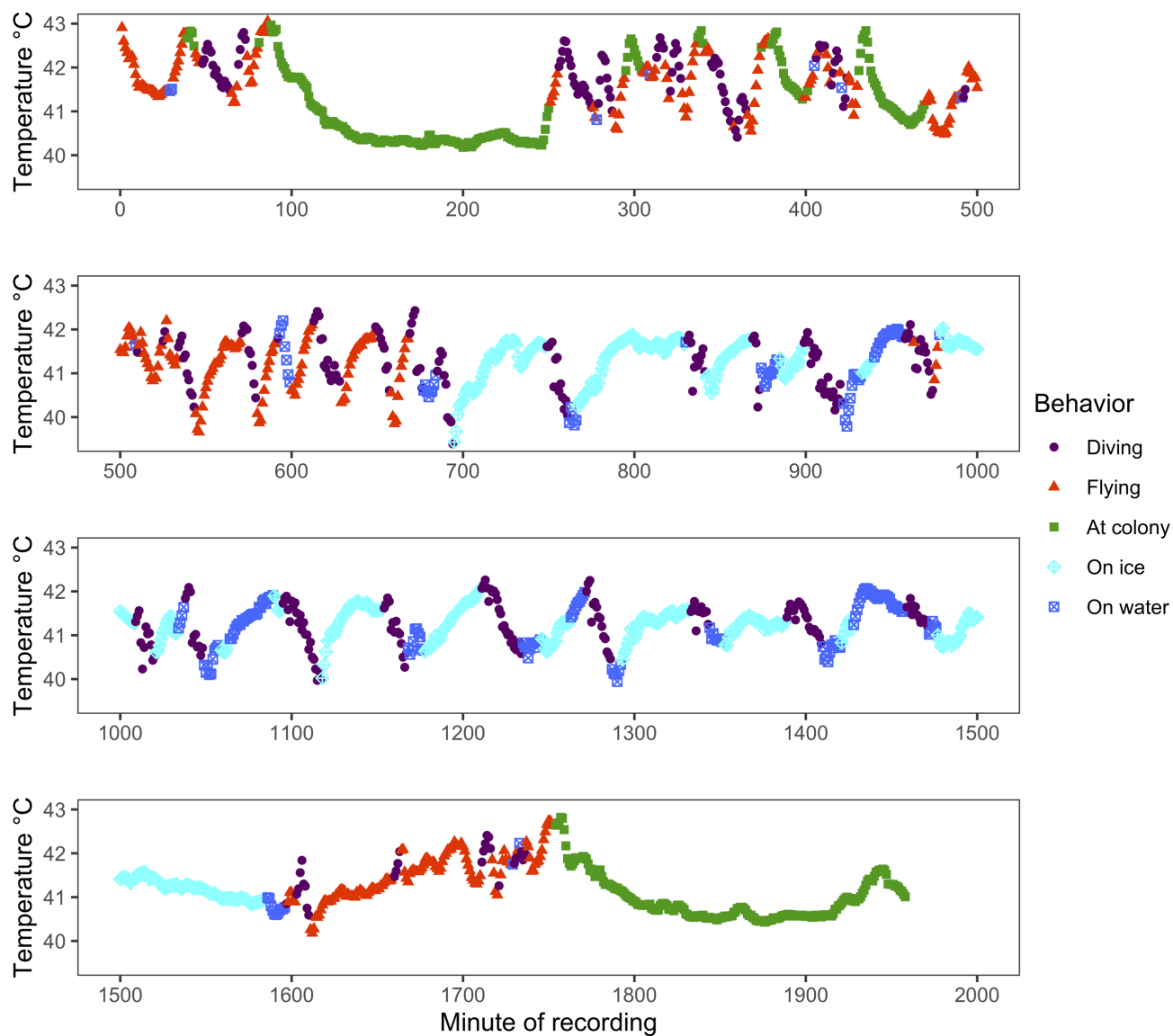
(a) Behavioral state	EM mean $\pm$ SE [CI]		
Diving (D)	$41.15 \pm 0.046$ [41.06, 41.24]		
Flying (F)	$41.27 \pm 0.043$ [41.18, 41.35]		
Colony (C)	$41.64 \pm 0.050$ [41.54, 41.74]		
Ice (I)	$40.96 \pm 0.056$ [40.85, 41.07]		
Water (W)	$41.14 \pm 0.051$ [41.04, 41.24]		
(b) Pairwise			
contrast	Estimate $\pm$ SE	$T$	$P$
D-F	$-0.121 \pm 0.038$	-3.192	0.012
D-C	$-0.495 \pm 0.054$	-9.157	<0.001
D-I	$0.189 \pm 0.050$	3.752	0.002

D-W	0.008 ± 0.043	0.187	0.999
F-C	-0.374 ± 0.053	-7.128	<0.001
F-I	0.310 ± 0.050	6.156	<0.001
F-W	0.129 ± 0.043	3.019	0.021
C-I	0.685 ± 0.063	10.92	<0.001
C-W	0.503 ± 0.058	8.616	<0.001
I-W	-0.181 ± 0.053	-3.371	0.007

219

---

220 **Effect of environmental conditions on mean  $T_b$ :** The best model predicting mean  $T_b$  included positive  
221 effects of ambient temperature ( $\beta \pm SE = 0.008 \pm 0.004$ ,  $T = 2.012$ ,  $P = 0.044$ ; Fig. 2a) and relative  
222 humidity ( $\beta \pm SE = 0.006 \pm 0.001$ ,  $T = 4.353$ ,  $P < 0.001$ ; Fig. 2b). The two-way interactions between  
223 ambient temperature, relative humidity and behavioral state were non-significant ( $F_4 = 1.853$ ,  $P = 0.116$ ;  
224  $F_4 = 0.878$ ,  $P = 0.476$ , respectively; Fig. 2a,b). There was a marginally significant interaction between  
225 wind speed and behavioral state in predicting  $T_b$  ( $F_4 = 2.302$ ,  $P = 0.056$ ; Fig. 2c). We proceeded to assess  
226 the meaning of this interaction by constructing models predicting the effect of wind speed within each  
227 behavioral state. The  $T_b$  of little auks increased with wind speed when birds were in flight, but did not  
228 vary with wind speed in the other behavioral states (Table 2a; Fig. 2c; see Table S1 for statistics for  
229 pairwise comparisons in the trends between behavioral states).



230

231 **Figure 1.** Variation in body temperature ( $T_b$ ) through time and color coded with respect to behavioral  
232 state for one individual little auk (LIAK20EG19) from the Ukaleqarteq, East Greenland, population. Note  
233 rebounds in  $T_b$  when on the sea ice following declines while diving in cold arctic waters.  $T_b$  can also be  
234 observed to increase with time during flight and decline with time at the colony.

235

236

237

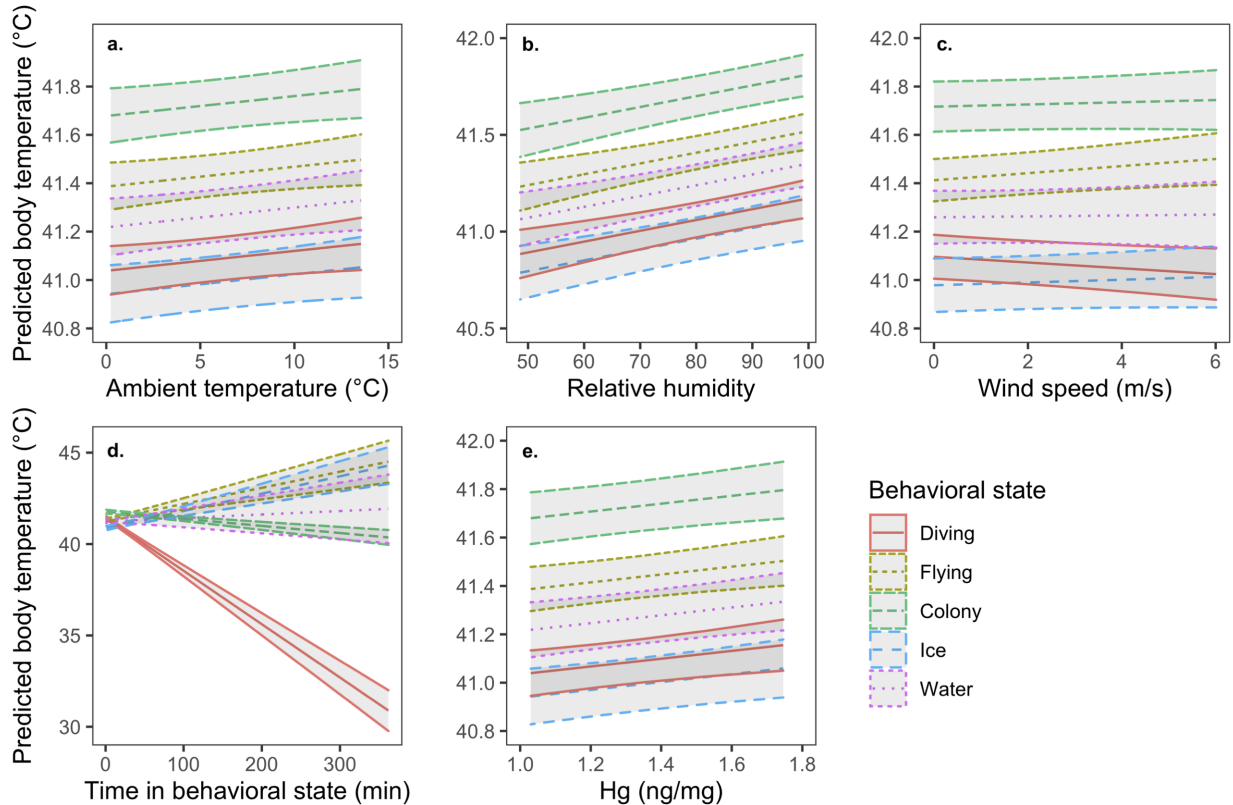
238 **Table 2.** Results of GAMMs predicting  $T_b$  within the behavioral states, showing estimated effects  
 239 (Estimate  $\pm$  SE, t, P) of wind speed (m/s) (a), and time interval (min) within the behavioral bought (b).  
 240 Differences in superscript letters indicate significant differences between trends.

	(a) Wind speed	(b) Time interval
Diving	-0.007 $\pm$ 0.008, -0.853, 0.393 <sup>a</sup>	-0.024 $\pm$ 0.001, -15.15, <0.001 <sup>a</sup>
Colony	0.001 $\pm$ 0.005, 0.110, 0.913 <sup>a,c</sup>	-0.004 $\pm$ 0.001, -5.807, <0.001 <sup>b</sup>
Ice	0.004 $\pm$ 0.004, 1.193, 0.233 <sup>a,c</sup>	0.014 $\pm$ 0.001, 12.36, <0.001 <sup>c</sup>
Flying	0.015 $\pm$ 0.007, 2.265, 0.0236 <sup>a,c</sup>	0.001 $\pm$ 0.0001, 1.580, 0.114 <sup>c</sup>
Water	0.001 $\pm$ 0.009, 0.148, 0.882 <sup>b,c</sup>	0.001 $\pm$ 0.003, 0.549, 0.583 <sup>b,c</sup>

241  
 242 **Interaction with time in the behavioral state in predicting mean  $T_b$  and  $\Delta T_b$ :** In addition, the best  
 243 model predicting the mean  $T_b$  of little auks included the interaction between behavioral state and time  
 244 interval within the behavior state ( $F_4=49.23$ ,  $P < 0.001$ ; Fig. 1; Fig. 2d). We proceeded to assess the  
 245 meaning of this interaction by constructing models predicting the effect of time interval within each  
 246 behavioral state. The  $T_b$  of little auks decreased with the amount of time spent diving, or at the colony  
 247 (Table 2b; Fig. 1; Fig. 2d). In contrast,  $T_b$  increased the longer birds spent on the sea ice and tended to  
 248 increase during flight (Table 2b; Fig. 1; Fig. 2d).  $T_b$  did not consistently vary with time when birds were  
 249 resting on the water surface (Table 2b; Fig. 1; Fig. 2d; see Table S2 for statistics for pairwise  
 250 comparisons in trends between behavioral states).

251 Results regarding the  $\Delta T_{bs}$  for the different behavioral states mostly aligned with the analysis above  
 252 (Table S3). The  $\Delta T_b$  for diving was negative, with the 95% CI not overlapping zero, and was significantly  
 253 lower than all other delta  $T_{bs}$ . In contrast, the  $\Delta T_b$  for flying and resting on the sea ice were positive, with  
 254 the CIs not overlapping zero, and were significantly higher than all other delta  $T_{bs}$ , with the  $\Delta T_b$  for sea ice  
 255 also greater than that of flying. The  $\Delta T_b$  for at the colony and on the water were negative, and positive,

256 respectively, but did not significantly differ from each other or from zero (CIs overlapping zero) (Table  
257 S3),  
258



259  
260 **Figure 2.** Relationships between the mean  $T_b$  of little auks and (a) ambient temperature, (b) relative  
261 humidity, (c) wind speed, (d) time within the behavioral state, and (e) mercury concentrations. The effect  
262 of wind speed and time in behavioral state on  $T_b$  varied with behavioral state, whereas the effects of the  
263 other variables were consistent across behavioral states.

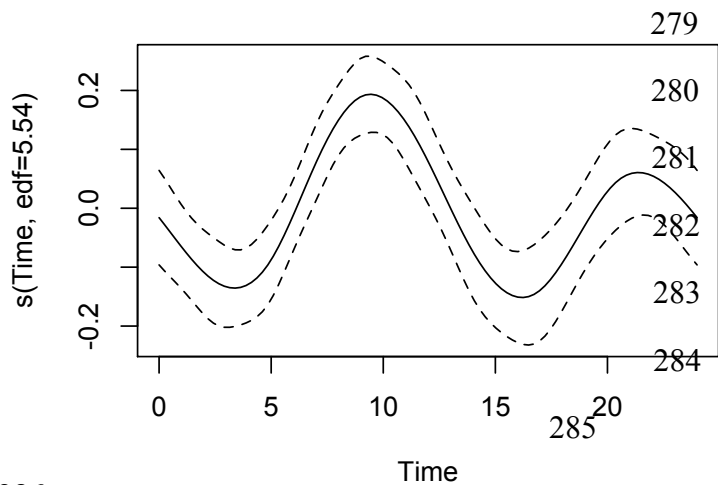
264  
265 **The effect of Hg on mean  $T_b$ :** The mean  $\pm$  SE Hg concentration in the blood was  $1.290 \pm 0.031 \mu\text{g g}^{-1}$   
266 dw [range: 1.030-1.746  $\mu\text{g g}^{-1}$  dw], which assuming 79% blood moisture content is equivalent to  $0.271 \pm$   
267  $0.007 \mu\text{g g}^{-1}$  ww [range: 0.216-0.367  $\mu\text{g g}^{-1}$  ww], and falls within the range of low risk for toxicological  
268 effects (0.2–1.0  $\mu\text{g g}^{-1}$  ww; Ackerman et al. 2016). Independent of behavioral state or weather conditions,  
269 the  $T_b$  of little auks was significantly higher in birds with higher Hg levels ( $\beta \pm \text{SE} = 0.161 \pm 0.061$ ,  $t =$

270 2.639,  $P = 0.008$ ; Fig. 2e). Hg levels did not significantly interact with behavioral state ( $F_4 = 1.811$ ;  $P =$   
271 0.124), ambient temperature ( $F_1 = 0.373$ ,  $P = 0.542$ ), relative humidity ( $F_1 = 0.199$ ,  $P = 0.655$ ), or wind  
272 speed ( $F_1 = 0.056$ ,  $P = 0.812$ ) to predict  $T_b$ .

273

274 **Effect of time of day on mean  $T_b$ :** Mean  $T_b$  varied over the 24 hour period, with the best model  
275 including a highly non-linear ( $\text{edf} > 2$ ) cyclic smooth spline term for the effect of time ( $\text{edf} = 5.544$ ,  $F_8 =$   
276 77.858,  $P < 0.001$ ; Fig. 2). The spline term suggested a peak in  $T_b$  around mid-day (~10:00-15:00) and  
277 the lowest values in the early morning (~4:00 am) (Fig. 3).

278



279 **Figure 3.** Residuals from the gamm model  
280 predicting mean  $T_b$  from time of day, with a  
281 smooth curve fitted. Dashed lines show 2-SE  
282 limits. The y-axis shows the partial effect of time  
283 on  $T_b$ .

286

287 **Effect of behavioral state on between minute variation in  $T_b$ :** The mean  $\pm$  SD of between minute  
288 variation in  $T_b$ , as quantified by the absolute value of the difference between consecutive 1 minute  
289 readings, was  $0.089 \pm 0.106$  (range: 0-1.46). Variation was highest when birds were foraging at sea,  
290 followed by flying, resting on the water surface, at the colony and on the sea ice (Table 3). There were  
291 significant differences in the between minute variation in  $T_b$  between behavioral states, with the exception  
292 of when birds were in flight and resting on the water surface (Table 3).

293

294 **Effect of environmental conditions on between minute variation in  $T_b$ :** The best model describing  
295 between minute variation in  $T_b$  included a positive effect of ambient temperature ( $\beta \pm SE = 0.003 \pm 0.001$ ,  
296  $T = 4.212$ ,  $P < 0.001$ ; Fig. 4a). There was also a significant interaction between wind speed and  
297 behavioral state in predicting variation in  $T_b$  ( $F_4 = 4.99$ ,  $P < 0.001$ ; Fig. 4b). Again, we assessed the  
298 meaning of this interaction by constructing models predicting the effect of wind speed within each  
299 behavioral state. Variation in  $T_b$  increased with wind speed when birds were diving and flying. In  
300 contrast, wind speed was not significantly related to variation in  $T_b$  when birds were at the colony, on the  
301 sea ice, or resting on the water surface, and the coefficient estimate within these behavioral states was  
302 negative (Table 4a; see Table S4 for statistics for pairwise comparisons in the trends between behavioral  
303 states). Relative humidity was not related to variation in  $T_b$  ( $\beta \pm SE = 0.0001 \pm 0.0003$ ,  $T = 0.351$ ,  $P =$   
304  $0.723$ ), and the interactions between ambient temperature, relative humidity, and behavioral state were  
305 non-significant ( $F_4 = 0.096$ ,  $P = 0.983$ ;  $F_4 = 0.052$ ,  $P = 0.995$ ; respectively).

306

307 **Interaction with time in the behavioral state in predicting between minute variation in  $T_b$ :** As for  
308 mean  $T_b$ , there was an interaction between time interval within the behavioral state and behavioral state in  
309 predicting between minute variation in  $T_b$  ( $F_4 = 75.77$ ,  $P < 0.001$ ; Fig. 4c). Models constructed within the  
310 behavioral states indicated that between minute variation in  $T_b$  decreased with time in the behavioral state  
311 for all behaviors. However, this decrease was the steepest, and relatively equal in magnitude, when birds  
312 were resting in the water or engaged in diving bouts. The next steepest decrease was observed when birds  
313 were in flight, followed by when birds were on the sea ice, and the decrease was lowest when birds were  
314 at the colony (Table 4b; see Table S5 for statistics for pairwise comparisons in the trends between  
315 behaviors states).

316

317 **Table 3.** Between minute variation ( $|T_{b1}-T_{b1+1}|$ ) in  $T_b$  of little auks in the five behavioral states: (a)  
 318 estimated marginal (EM) means from the best-fitting GAMM with interactions removed ( $df=15127$ ), (b)  
 319 pairwise contrasts between behavioral states.

(a) Behavioral			
state	EM mean $\pm$ SE [CI]		
Diving (D)	0.156 $\pm$ 0.003 [0.149, 0.163]		
Flying (F)	0.118 $\pm$ 0.004 [0.110, 0.126]		
Colony (C)	0.091 $\pm$ 0.006 [0.079, 0.103]		
Ice (I)	0.063 $\pm$ 0.006 [0.052, 0.074]		
Water (W)	0.113 $\pm$ 0.005 [0.103, 0.124]		
(b) Pairwise			
contrast	Estimate $\pm$ SE	<i>T</i>	<i>P</i>
D-F	0.038 $\pm$ 0.055	6.890	<0.001
D-C	0.065 $\pm$ 0.007	9.023	<0.001
D-I	0.093 $\pm$ 0.006	14.18	<0.001
D-W	0.043 $\pm$ 0.006	6.663	<0.001
F-C	0.027 $\pm$ 0.008	3.622	0.003
F-I	0.055 $\pm$ 0.007	8.053	<0.001
F-W	0.005 $\pm$ 0.006	0.694	0.958
C-I	0.028 $\pm$ 0.008	3.381	0.007
C-W	-0.023 $\pm$ 0.008	-2.759	0.046
I-W	-0.051 $\pm$ 0.008	-6.683	<0.001

320

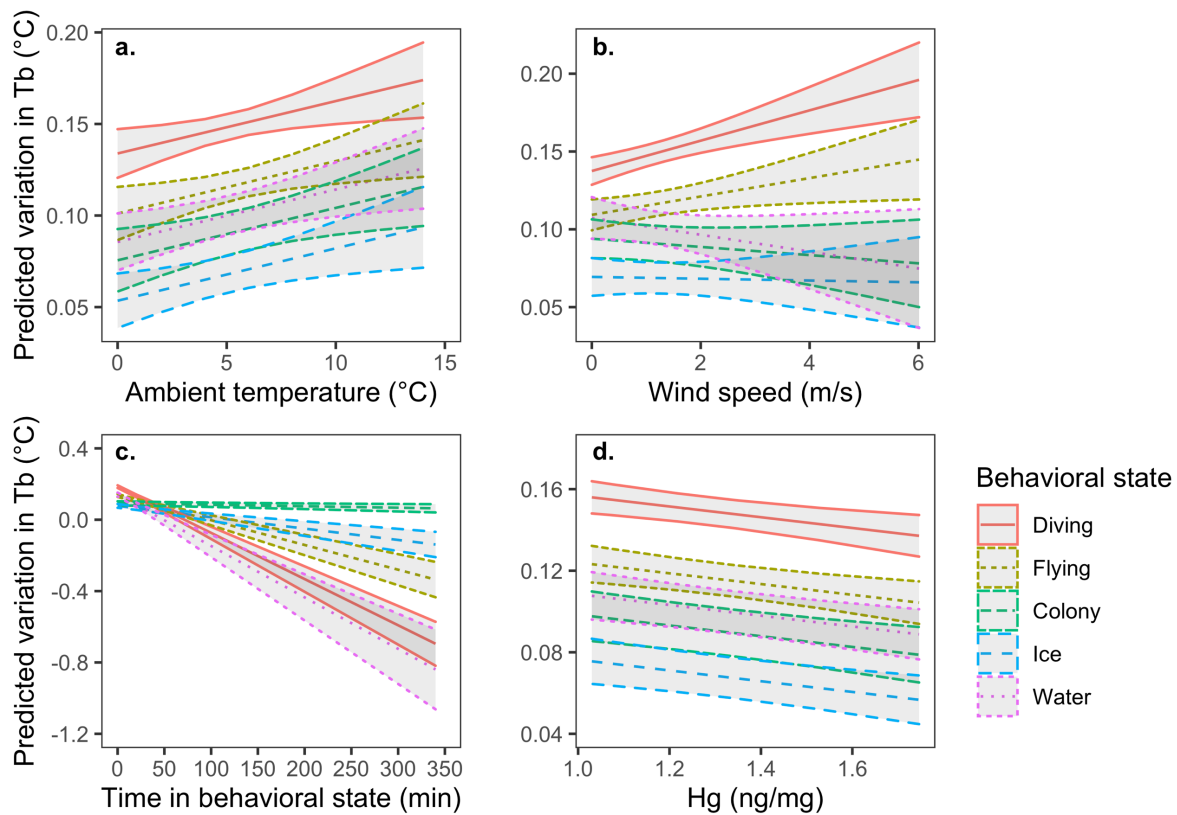


321 **Table 4.** Results of GAMMs predicting variation ( $|T_{b1}-T_{b1+1}|$ ) in  $T_b$  within the behavioral states, showing  
 322 estimated effects (Estimate  $\pm$  SE, t, P) of wind speed (m/s) (a), and time interval (min) within the  
 323 behavioral bought (b). Differences in superscript letters indicate significant differences between trends.

	(a) Wind speed	(b) Time interval
Diving	0.009 $\pm$ 0.003, 3.054, 0.002 <sup>a</sup>	-0.003 $\pm$ 0.0002, -10.99, <0.001 <sup>a</sup>
Colony	-0.003 $\pm$ 0.002, -1.690, 0.091 <sup>b</sup>	-0.0001 $\pm$ 0.0003, -2.586, 0.009 <sup>b</sup>
Ice	-0.001 $\pm$ 0.002, -0.533, 0.594 <sup>b</sup>	-0.0006 $\pm$ 0.0001, -9.966, <0.001 <sup>c</sup>
Flying	0.007 $\pm$ 0.003, 2.585, 0.010 <sup>a,b</sup>	-0.002 $\pm$ 0.0002, -8.580, <0.001 <sup>d</sup>
Water	-0.006 $\pm$ 0.004, -1.608, 0.108 <sup>b</sup>	-0.003 $\pm$ 0.0004, -8.557, <0.001 <sup>a</sup>

324

325



326

327 **Figure 4.** Relationships between the between minute variation in  $T_b$  of little auks and (a) ambient  
328 temperature, (b) wind speed, (c) time within the behavioral state, and (e) mercury concentrations. The  
329 effect of wind speed and time in behavioral state on  $T_b$  varied with behavioral state, whereas the effects of  
330 the other variables were consistent across behavioral states.

331  
332 **The effect of mercury on between minute variation in  $T_b$ :** Mercury concentrations in the blood did not  
333 significantly interact with behavioral state ( $F_4 = 0.842$ ;  $P = 0.498$ ), ambient temperature ( $F_1 = 0.373$ ,  $P =$   
334  $0.542$ ), relative humidity ( $F_1 = 3.154$ ,  $P = 0.076$ ), or wind speed ( $F_1 = 0.214$ ,  $P = 0.643$ ) to predict  
335 between minute variation in  $T_b$ . However, independent of behavioral state or weather conditions,  
336 between minute variation in the  $T_b$  of little auks was significantly lower in birds with higher Hg levels ( $\beta$   
337  $\pm$  SE =  $-0.026 \pm 0.008$ ,  $t = -3.193$ ,  $P = 0.001$ ; Fig. 4d).

338  
339 **Effect of time of day on between minute variation in  $T_b$ :** Between minute variation in  $T_b$  did not vary  
340 with time of day (edf = 0.949,  $F_8 = 0.226$ ,  $P = 0.127$ ).

## 341 342 **Discussion**

343 Although  $T_b$  in little auks was relatively tightly regulated around a mean of 41.02 °C, we observed low,  
344 but significant, variation according to behavioral state and weather conditions. Such plasticity may be  
345 critical to maintaining energy balance across contexts and may buffer species against negative fitness  
346 effects in the context of global change. Nevertheless, the potential for plasticity to prevent energetic costs  
347 is not infinite, and our study suggested potential thermoregulatory challenges under global climate change  
348 scenarios. In particular,  $T_b$  rebounded on sea ice following declines during diving episodes in frigid Arctic  
349 waters, suggesting that loss of this resting substrate may elevate thermoregulatory costs, negatively  
350 affecting energy balance, body condition, and/or fitness. In addition, we tested whether exposure of little  
351 auks to Hg interacted with environmental conditions to affect  $T_b$ . Hg is an important chemical

352 contaminant in the Arctic, and has the potential to disrupt thermoregulatory processes, for instance  
353 through endocrine disruption, or by imposing detoxification challenges. No interactive effects between  
354 Hg exposure and environmental conditions were detected. However, a concerning contingency is that the  
355 higher, less variable,  $T_b$  observed in more contaminated birds could limit plasticity and/or pose energetic  
356 challenges under future scenarios of global change.

357 The most exciting finding of our study was that  $T_b$  rebounded when birds were resting on sea ice,  
358 following declines while foraging in cold Arctic waters. Specifically, average  $T_b$  on the sea ice was  
359 actually lower than in any other behavioral state, which we believe reflects the fact that birds exit the  
360 water when their  $T_b$  falls below a threshold. While resting on sea ice, birds increased their  $T_b$  by an  
361 average of  $\sim 0.33^\circ\text{C}$ , meaning that, on average, they approximately recovered the amount of  $T_b$  lost while  
362 foraging, that is,  $\sim 0.31^\circ\text{C}$ . In contrast, while resting on the water surface,  $T_b$  remained relatively  
363 unchanged and did not differ significantly from when birds were foraging. Furthermore, the lowest  
364 variation in  $T_b$  was observed when birds were resting on sea ice, whereas the highest was observed during  
365 bouts of diving behavior, supporting the hypothesis that sea ice plays an important role in allowing birds  
366 to restore and maintain normiothermic temperatures after thermally challenging foraging bouts.

367 In the context of climate change, loss of sea ice may have significant energetic and thermoregulatory  
368 implications, as birds are forced to instead rest on the water surface. Birds face increased  
369 thermoregulatory challenges when in the water, which has much higher ( $\sim 25 \times$ ) thermal conductivity than  
370 air (Grémillet et al. 2015). In auks, compression of air space in the feathers while diving significantly  
371 reduces insulative properties, further facilitating heat exchange with the environment (Oswald and Arnold  
372 2012). Thus, birds resting on the water likely elevate their metabolic rate, even considering lower  $T_b$ ,  
373 which, *in lieu* of compensatory changes in behavior or physiology, could elevate daily energy expenditure  
374 and threaten to result in negative energy balance (Lovvorn et al. 2009). In addition, if  $T_b$  does not increase  
375 while resting on the water, but does when birds are at rest on sea ice, this could force birds to return to the  
376 colony sooner, limiting time for energy acquisition. Loss of sea ice as a substrate for resting, foraging,  
377 and movement has demonstrated effects on energy balance and population dynamics in many sea ice-

378 dependent species (Post et al. 2013; Laidre et al. 2020; Pagano and Williams 2021). For instance, polar  
379 bears (*Ursus maritimus*) and narwhal (*Monodon monoceros*), which both have foraging ecologies tightly  
380 with sea ice, show substantial elevations in locomotory costs (3-4 times greater) in association with sea  
381 ice declines (Pagano and Williams 2021). However, effects of sea ice loss on thermoregulatory dynamics  
382 have been under-explored.

383 A second major result of our study was demonstrating sensitivity of little auks'  $T_b$  to external  
384 environmental conditions, which may have implications under global change scenarios. Mean  $T_b$   
385 increased with ambient temperature and relative humidity, with these relationships consistent across  
386 behavioral states. As ambient temperature and relative humidity rise, the capacity for evaporative heat  
387 dissipation decreases, which may result in increases in  $T_b$  or elevated thermoregulatory costs to maintain  
388 optimal  $T_b$  (Dawson 182; Gerson et al. 2014). In contrast,  $T_b$  increased with wind speed only when birds  
389 were in flight, demonstrating that high winds increase the thermal challenges of flying, but have little  
390 effect on thermodynamics during other activities. With respect to the environmental-sensitivity of  
391 between minute variation in  $T_b$ , we observed an increase with ambient temperature, independent of  
392 behavioral state, suggesting that these cold-adapted birds face increasing challenges maintaining a stable  
393  $T_b$  at higher temperatures. In addition, as for mean  $T_b$ , we observed an interaction between wind speed and  
394 behavioral state, with between minute variation in  $T_b$  increasing with wind speed when birds were diving  
395 and flying, perhaps reflecting increased energetic and thermal challenges associated with activity during  
396 high winds. In contrast, wind speed was not strongly related to variation in  $T_b$  during the other behavioral  
397 states, which entail lower activity levels. In the context of climate change, these results suggest that  
398 alterations in ambient temperature may have implications for  $T_b$  regulation that are relatively independent  
399 of behavioral state, whereas changes in wind patterns may have especially high costs during active  
400 periods, especially during flight.

401 A third important finding of our study was that mean levels, and between minute variation, in  $T_b$  varied  
402 with concentrations of Hg in the blood. Independent of behavioral state,  $T_b$  increased with Hg levels. The  
403 elevation in  $T_b$  observed in birds with higher Hg levels could reflect an elevation in basal metabolic rate

404 (BMR) as a result of detoxification costs, such as those associated with depuration (Gerson et al. 2019b).  
405 The association between Hg exposure and BMR remains poorly explored and equivocal in wildlife  
406 (Chastel et al. 2022), and in the only study to invest the relationship between Hg contamination and BMR  
407 in Arctic birds, Hg was unassociated with BMR (Blévin et al. 2017). However, in a laboratory study on  
408 zebra finch (*Taeniopygia guttata*), exposure to environmentally-relevant levels of MeHg were associated  
409 with elevated BMR (Gerson et al. 2019b). To our knowledge, there is no previous study documenting a  
410 link between Hg concentration and  $T_b$  in free-ranging animals. However, contrary to our results, studies in  
411 laboratory animals have demonstrated hypothermic responses to Hg exposure, for instance, in the mouse  
412 (*Mus musculus*) (Gordon et al. 1990). Hypothermic responses to chemical contamination are hypothesized  
413 to reduce the toxicity of the contaminant in the body (Leon 2008), but may not be relevant at the  
414 relatively low Hg levels in our little auk population. In addition, since our results are correlational, the  
415 association between Hg contamination levels and  $T_b$  could be indirect, for instance, reflecting a higher  
416 rate of Hg accumulation in individuals with intrinsic differences in BMR and feeding rate.

417 In contrast to for mean  $T_b$ , we observed a negative relationship between Hg levels and minute-by-  
418 minute variation in  $T_b$ , which is inconsistent with the hypothesis that contaminated bird could have more  
419 difficulty maintaining a stable  $T_b$ . Moreover, Hg levels did not interact with environmental conditions to  
420 affect  $T_b$ , thus providing no evidence that exposure to this contaminant accentuates thermoregulatory  
421 responses to environmental change. However, absence of such interactive effects could reflect limitations  
422 to the range of Hg levels and environmental conditions spanned by our study. There is need for more  
423 research to examine the potential for interactive effects at higher contamination levels, and across steeper  
424 environmental gradients.

425 In addition to these central findings, our results suggested that the colony, as well as sea ice, serves as a  
426 thermal refuge for little auks, and indeed, may be selected for thermo-protective properties. The highest  
427 average levels of  $T_b$  were observed while birds were at the colony, even higher than when birds were in  
428 flight. Furthermore, the second lowest between minute variation in  $T_b$  occurred at the colony, which is  
429 consistent with the colony providing stable thermal conditions for birds. Higher average  $T_b$  at the colony

430 than when in flight, which opposes our predictions, may be due to a combination of factors. First, little  
431 auks occupy a relatively cold environment in which thermoregulatory substitution may occur. That is,  
432 heat generated in flight may offset thermoregulatory costs, reducing changes in  $T_b$  with activity (Careau  
433 and Garland 2012). Second, birds at the colony may be buffered from the effects of movement and wind  
434 exposure that disrupt the boundary layer and increase heat flux from the body. However,  $T_b$  did decrease  
435 slightly the longer birds spent at the colony, which may reflect an adaptive downregulation in resting  
436 birds or decreases in  $T_b$  following commuting flights between foraging sites and the colony.

437 As expected, we observed that  $T_b$  was higher when little auks were flying than when they were diving  
438 or resting on the water. Furthermore, although mean  $T_b$  in flight was lower than at the colony,  $T_b$  in flight  
439 increased, suggesting that heat generated during flight does increase  $T_b$ . For little auks, this pattern is  
440 expected due to their unique morphology. Little auks can be described as bullets with wings. They flap or  
441 fall. Their morphology and flight mode are characterized by high wing loadings and rapid wing beats,  
442 which translates into high flight costs (estimated at  $\sim 7.24 \times$  basal metabolic rate; Ste-Marie et al. 2022).

443 Also in-line with expectations, and discussed to some extent above, we observed that the  $T_b$  declined  
444 while little auks were foraging in cold waters. This decline in  $T_b$  may facilitate aerobic capacity during  
445 diving and limit heat loss, but may also reflect unavoidable declines linked to submergence in cold water  
446 with a high thermal conductance (Kooyman and Ponganis 1998; Favilla and Costa 2020; Williams and  
447 Ponganis 2021). In addition, declines in  $T_b$  while foraging may be magnified by ingestion of cold prey  
448 items. Indeed, ingestion-linked declines in  $T_b$  have been used to identify feeding events by past studies  
449 (Wilson et al. 1995). Our  $T_b$  data was logged at 1-min intervals, and thus lacked the resolution necessary  
450 to identify changes in  $T_b$  associated with independent feeding events. In another species of Alcid, the  
451 Brünnich's guillemots (*Uria lomvia*),  $T_b$  was observed to decline over the course of sequential diving  
452 bouts, as we see in the little auks. However, this decline occurred during periods resting on the water  
453 between dives, rather than during dives themselves. In the guillemots,  $T_b$  increased during dives, while the  
454 temperature of the periphery declined. This pattern contrasts to the declines in  $T_b$  during diving which  
455 have been observed in some species of penguins (Bevan et al. 2002; Green et al. 2003; Williams and

456 Ponganis 2021), and was interpreted as reflecting a combination of peripheral vasoconstriction and high  
457 wing beat frequency that generates heat (Niizuma et al. 2007). Our data lack the resolution to effectively  
458 separate dives from inter-dive intervals. Thus, a similar dynamic could also be occurring in our birds.

459 Finally, the best model predicting mean  $T_b$  included a non-linear effect of time, with the highest values  
460 occurring around mid-day and the lowest values in the early morning. Despite the fact that little auks in  
461 our population breed under 24-hrs of daylight, this diurnal variation in  $T_b$  may reflect timing of maximum  
462 solar radiation exposure, a diel pattern of activity levels, and/or underlying circadian rhythmicity in  $T_b$   
463 independent of activity levels. A past study on little auks found a regular rhythm of population attendance  
464 at the population level, likely associated with period of lower predation pressure, which provides some  
465 foundation for expecting that  $T_b$  could also display a diel pattern of variation. However, this same study  
466 found little circadian rhythm in activity patterns of individual little auks (Wojczulanis-Jakubas et al.  
467 2020), In contrast to mean  $T_b$ , between minute variation in  $T_b$  did not show a pattern with time of day.

468  
469 **Conclusions:** Our results demonstrate that the  $T_b$  of little auks is modulated according to both behavioral  
470 state and environmental conditions, which likely aids animals in maximizing energy balance while  
471 performing essential behaviors in dynamic environments. Although this plasticity is predicted to facilitate  
472 energy balance in the face of climate change, the dynamic nature of  $T_b$  regulation also suggests that  
473 changing environmental conditions may significantly alter energy balance, or the behavioral and energetic  
474 strategies that must be adopted to achieve energetic homeostasis. Most notably, our data suggests that  
475 little auks use sea ice as a thermal refuge, resting on this substrate to allow  $T_b$  to rebound after submersion  
476 in cold water. If sea ice is lost due to warming temperature, thermoregulatory costs are forecast to  
477 increase substantially as birds are forced to instead rest on the water surface. Furthermore, the elevated  
478 and less variable  $T_b$  of little auks with high Hg concentrations is of potential concern. Higher  $T_b$  in  
479 contaminated birds could elevate energetic costs or limit plasticity, further challenging scope for  
480 maintaining energy balance under scenarios of environmental change.

481

482 **Data availability:** Data will be made available via the Zenodo community of European Commission  
483 Funded Research (OpenAIRE) (doi: 10.5281/zenodo.7220883).

484

485 **Acknowledgements:** We thank Valère Marsaudon for his help with data collection in East Greenland,  
486 and members of Nanu travel for logistical support. We are grateful to Clément Bertin for aid in extracting  
487 sea ice coverage data. MLG and ALG are supported by the European Union's Horizon 2020 programme  
488 (Marie Skłodowska-Curie grants 101025549, 896866). We acknowledge long-term support from the  
489 French Polar Institute (IPEV), through the ADACLIM program (388) administered by JF and DG. This  
490 work contributes to research projects ARCTIC-STRESSORS and ILETOP funded by the French National  
491 Research Agency (ANR-20-CE34-0006, ANR-16-CE34-0005), the international initiative ARCTOX  
492 ([arctox.cnrs.fr](http://arctox.cnrs.fr)) and the Excellence Chair ECOMM funded by the Region Nouvelle Aquitaine.

493

494 **Conflict of Interest:** The authors have no conflicts of interest to declare.

495

496 **Authors' contributions:** MLG, ASG and JF conceived the study. MLG, ASG, DG and JF obtained  
497 funding for fieldwork and laboratory analyses. MSG, ALG, SG and JF collected the data. MLG, ASG and  
498 AS analysed the data. MLG and ASG wrote the first draft of the manuscript. All authors read and  
499 commented on the manuscript.

500

## 501 **References**

502 Ackerman JT, Eagles-Smith CA, Herzog MP, Hartman CA, Peterson SH, Evers DC, et al. 2016. Avian  
503 mercury exposure and toxicological risk across western North America: a synthesis. *Sci Total*  
504 *Environ.* 568: 749-769.

505 Albert C, Renedo M, Bustamante P, Fort J. 2019. Using blood and feathers to investigate large-scale Hg  
506 contamination in Arctic seabirds: a review. *Environ Res.* 177: 108588. doi:

507 [10.1016/j.envres.2019.108588](https://doi.org/10.1016/j.envres.2019.108588).



- 508 AMAP, 2021. 2021. AMAP Mercury Assessment. Summary for Policy-makers. Arctic Monitoring and  
509 Assessment Programme (AMAP), Tromsø, Norway. 16 pp.
- 510 Amélineau F, Grémillet D, Harding AMA, Walkusz W, Choquet R, Fort J. 2018. Arctic climate change  
511 and pollution impact little auk foraging and fitness across a decade. *Sci Rep.* 9: 1014. doi:  
512 10.1038/s41598-018-38042-z.
- 513 Angilletta MJ, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal physiology in  
514 endotherms. *Front Biosci E2*: 861–881. ddoi: 10.2741/e148.
- 515 Aulie A. 1971. Body temperatures in pigeons and budgerigars during sustained flight. *Comp Biochem*  
516 *Physiol A.* 39: 173-176. doi: 10.1016/0300-9629(71)90074-0.
- 517 Bevan RM, Butler PJ, Woakes AJ, Boyd IL. 2002. The energetics of gentoo penguins, *Pygoscelis papua*,  
518 during the breeding season. *Funct Ecol.* 16: 175–190. doi:10.1046/j.1365-2435.2002.00622.x.
- 519 Blévin P, Tartu S, Ellis HI, Chastel O, Bustamante P, Parenteau C, Herzke D, Angelier F, Gabrielsen  
520 GW. 2017. Contaminants and energy expenditure in an Arctic seabird: Organochlorine pesticides  
521 and perfluoroalkyl substances are associated with metabolic rate in a contrasted manner. *Environ*  
522 *Res.* 157: 118–126. doi: 10.1016/j.envres.2017.05.022.
- 523 Brodin A, Nilsson JÅ, Nord A. 2017. Adaptive temperature regulation in the little bird in winter:  
524 predictions from a stochastic dynamic programming model. *Oecologia* 185: 43-54. doi:  
525 10.1007/s00442-017-3923-3.
- 526 Bruinzeel LW, Piersma T. 2008. Cost reduction in the cold: heat generated by terrestrial locomotion  
527 partly substitutes for thermoregulatory costs in Knot *Calidris canutus*. *Ibis* 140: 323-328. doi:  
528 10.1111/j.1474-919X.1998.tb04396.x.
- 529 Bustamante P, Lahaye V, Durnez C, Churlaud C, Caurant, F. 2006. Total and organic Hg concentrations in  
530 cephalopods from the North Eastern Atlantic waters: Influence of geographical origin and feeding  
531 ecology. *Sci Total Environ.* 368: 585–596. doi: 10.1016/j.scitotenv.2006.01.038.
- 532 Calow P. 1991. Physiological costs of combating chemical toxicants - ecological implications. *Comp*  
533 *Biochem Physiol C Comp Pharmacol Toxicol.* 100: 3-6. doi: 10.1016/0742-8413(91)90110-f.

- 534 Careau V, Garland Jr. T. 2012. Performance, personality, and energetics: Correlation, causation, and  
535 mechanism. *Physiol Biochem Zool.* 85: 543– 571. doi: 10.1086/666970.
- 536 Chastel O, Fort J, Ackerman JT, Albert C, Angelier F, Basu N, *et al.* 2022. Mercury contamination and  
537 potential health risks to Arctic seabirds and shorebirds. *Sci Total Environ.* 844: 156944. doi:  
538 10.1016/j.scitotenv.2022.156944.
- 539 Cooper CE, Hurley LL, Deviche P, Griffith SC. 2020. Physiological responses of wild zebra finch  
540 (*Taeniopygia guttata*) to heatwaves. *J Exp Biol.* 223: jeb225524. doi: 10.1242/jeb.225524.
- 541 Crompton AW, Taylor CR, Jagger JA. 1978. Evolution of homeothermy in mammals. *Nature* 272: 333-  
542 336. doi:10.1038/272333a0.
- 543 Dawson WR. 1982. Evaporative losses of water by birds. *Comp Biochem Physiol A* 71: 495-509. doi:  
544 10.1016/0300-9629(82)90198-0.
- 545 Douglas TK, Cooper CE, Withers PC. 2017. Avian torpor or alternative thermoregulatory strategies for  
546 overwintering? *J Exp Biol.* 220: 1341-1349. doi:10.1242/jeb.154633.
- 547 Enstipp MR, Grémillet D, Lorentsen S-H. 2005. Energetic costs of diving and thermal status in European  
548 shags (*Phalacrocorax aristotelis*). *J Exp Biol.* 208:3451-3461. doi:10.1242/jeb.01791.
- 549 Favilla AB, Costa DP. 2020. Thermoregulatory Strategies of Diving Air-Breathing Marine Vertebrates: A  
550 Review. *Front Ecol Evol.* 8: 555509. doi: 10.3389/fevo.2020.555509.
- 551 Fort J, Porter WP, Grémillet D. 2009. Thermodynamic modelling predicts energetic bottleneck for  
552 seabirds wintering in the northwest Atlantic. *J Exp Biol.* 212: 2483–2490. doi:  
553 10.1242/jeb.032300.
- 554 Fort J, Robertson GJ, Grémillet D, Traisnel G, Bustamante P. 2014. Spatial ecotoxicology: migratory  
555 seabirds are exposed to mercury contamination while overwintering in the Northwest Atlantic.  
556 *Environ Sci Technol.* 48: 11560-11567. doi: 10.1021/es504045g.
- 557 Gerson AR, Smith EK, Smit B, McKechnie AE, Wolf B. 2014. The impact of humidity on evaporative  
558 cooling in small desert birds exposed to high air temperature. *Physiol Biochem Zool.* 87: 782-  
559 795. doi: 10.1086/678956.

- 560 Gerson AR, McKechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, et al. 2019a. The functional  
561 significance of facultative hyperthermia varies with body size and phylogeny in birds. *Funct Ecol.*  
562 33: 597–607. doi: 10.1111/1365-2435.13274
- 563 Gerson AR, Cristol DA, Seewagen CL. 2019b. Environmentally relevant methylmercury exposure  
564 reduces the metabolic scope of a model songbird. *Environ Pollut.* 246: 790–796. doi:  
565 10.1016/j.envpol.2018.12.072.
- 566 Gordon CJ, Fogelson L, Highfill JW. 1990. Hypothermia and hypometabolism: Sensitive indices of  
567 whole-body toxicity following exposure to metallic salts in the mouse. *J Toxicol Environ Health*  
568 29: 185–200. doi: 10.1080/15287399009531382.
- 569 Green J, Butler P, Woakes A, Boyd I. 2003. Energetics of diving in macaroni penguins. *J Exp Biol.* 206:  
570 43–57. doi:10.1242/jeb.00059.
- 571 Grémillet D, Kuntz G, Woakes AJ, Gilbert C, Robin J-P, Le Maho, Y, Butler PJ. 2005. Year-round  
572 recordings of behavioural and physiological parameters reveal the survival strategy of a poorly  
573 insulated diving endotherm during the Arctic winter. *J Exp Biol.* 208: 4231–4241. doi:  
574 10.1242/jeb.01884.
- 575 Humphries MM, Careau V. 2011. Heat for nothing or activity for free? Evidence and implications for  
576 activity-thermoregulatory heat substitution. *Integ Comp Biol.* 51:419-431. doi:  
577 10.1093/icb/icr059.
- 578 Jenssen BM. 2006. Endocrine-disrupting chemicals and climate change: a worst-case combination for arctic  
579 marine mammals and seabirds? *Environ Health Persp.* 114: 76. doi: 10.1289/ehp.8057.
- 580 Jonsson S, Mastromonaco MN, Wang F, Bravo AG, Cairns WRL, Chételat J, et al. 2022. Arctic  
581 methylmercury cycling. *Sci Total Environ.* 850: 157445. doi: 10.1016/j.scitotenv.2022.157445.
- 582 Khaliq I, Hof C, Prinzing R, Böhning-Gaese K, Pfenninger M. 2014. Global variation in thermal  
583 tolerances and vulnerability of endotherms to climate change. *Proc Roy Soc London B.* 281:  
584 20141097. doi: 10.1098/rspb.2014.1097.

- 585 Kooyman GL, Ponganis PJ. 1998. The physiological basis of diving at depth: birds and mammals.  
586 *Ann Rev Physiol.* 60: 19–32. doi: 10.1146/annurev.physiol.60.1.19.
- 587 Laidre KL, Atkinson S, Regehr EV, Stern HL, Born EW, Wiig Ø, *et al.* 2020. Interrelated ecological  
588 impacts of climate change on an apex predator. *Ecol Appl.* 30: e02071. doi: 10.1002/eap.2071.
- 589 Lenth R. 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version  
590 1.4.3.01. <https://CRAN.R-project.org/package=emmeans>.
- 591 Leon LR. 2008. Thermoregulatory responses to environmental toxicants: The interaction of thermal stress  
592 and toxicant exposure. *Toxicol Appl Pharmacol.* 233: 146–161. doi: 10.1016/j.taap.2008.01.012.
- 593 Lovvorn JR, Grebmeier JM, Cooper LW, Bump JK, Richman SE. 2009. Modeling marine protected areas  
594 for threatened eiders in a climatically changing Bering Sea. *Ecol Appl.* 19: 1596–1613. doi:  
595 10.1890/08-1193.1.
- 596 Lüdtke D. 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J Open Sour*  
597 *Software* 3: 772. doi: 10.21105/joss.00772 (URL: <https://doi.org/10.21105/joss.00772>).
- 598 Luque, S.P. Diving Behaviour Analysis in R. *R News* 7: 8-14.
- 599 McKechnie AE, Lovegrove BG. 2002. Avian facultative hypothermic responses: a review. *The Condor*  
600 104: 705-724. doi:10.1093/condor/104.4.705.
- 601 McKechnie AE, Wolf BO. 2019. The physiology of heat tolerance in small endotherms. *Physiol.* 34: 302-  
602 313. doi: 10.1152/physiol.00011.2019.
- 603 Morel FMM, Kraepiel AML, Amyot M. 1998. The chemical cycle and bioaccumulation  
604 of mercury. *Annu Rev Ecol Syst.* 29: 543–566. doi: 10.1146/annurev.ecolsys.29.1.543.
- 605 Mori Y, Yoda K, Sato K. 2001. Defining dive bouts using a sequential differences analysis. *Behavior*  
606 138: 1451-1466. doi: 10.1163/156853901317367690.
- 607 Niizuma Y, Gabrielsen GW, Sato K, Watanuki Y, Naito Y. 2007. Brünnich’s guillemots (*Uria lomvia*)  
608 maintain high temperature in the body core during dives. *Comp Biochem Physiol Part A: Mol Int*  
609 *Physiol.* 147: 438–444. doi: 10.1016/j.cbpa.2007.01.014.

- 610 Nilsson JÅ, Molokwu MN, Olsson O. 2016. Body temperature regulation in hot environments. PLoS One  
611 11:e0161481. doi: 10.1371/journal.pone.0161481.
- 612 Noyes PD, McElwee MK, Miller HD, Clark BW, Van Tiem LAV, Walcott KC, Erwin KN, Levin ED.  
613 2009. The toxicology of climate change: environmental contaminants in a warming world.  
614 Environ Intern. 35: 971-986. doi: 10.1016/j.envint.2009.02.006.
- 615 Pagano AM, Williams TM. 2021. Physiological consequences of Arctic sea ice loss on large marine  
616 carnivores: Unique responses by polar bears and narwhals. J Exp Biol. 224(Suppl\_1): jeb228049.  
617 doi: 10.1242/jeb.228049.
- 618 Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2019. nlme: Linear and Nonlinear Mixed Effects  
619 Models. R package version 3.1-143, <URL: <https://CRAN.R-project.org/package=nlme>>.
- 620 Ponganis PJ, Van Dam RP, Levenson DH, Knowler T, Ponganis KV, Marshall G. 2003. Regional  
621 heterothermy and conservation of core temperature in emperor penguins diving under sea ice.  
622 Comp Biochem Physiol. Part A: Mol Int Physiol. 135: 477–487. doi: 10.1016/S1095-  
623 6433(03)00133-8.
- 624 Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, *et al.* 2013. Ecological consequences  
625 of sea-ice decline. Science 341: 519-524. doi: 10.1126/science.1235225.
- 626 R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for  
627 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 628 Rice KM, Walker EM Jr., Wu M, Gillette C, Blough ER. 2014. Environmental mercury and its toxic  
629 effects. J Prev Med Public Health 47: 74-83. doi: 10.3961/jpmph.2014.47.2.74.
- 630 Richman SE, Lovvorn JR. 2011. Effects of air and water temperatures on resting metabolism of auklets  
631 and other diving birds. Physiol Biochem Zool. 84: 31-332. doi:10.1086/660008.
- 632 Sibley R, Nott H, Fletcher D. 1990. Splitting behaviour into bouts. Anim Behav. 39: 63-69. doi:  
633 10.1016/S0003-3472(05)80726-2.
- 634 Stager M, Senner NR, Tobalske BW, Cheviron ZA. 2020. Body temperature maintenance acclimates in a  
635 winter-tenacious songbird. J Exp Biol. 223: jeb221853. doi: 10.1242/jeb.221853.

- 636 Ste-Marie E, Grémillet D, Fort J, Patterson A, Brisson-Curadeau É, Clairbaux M, Perret S, Speakman JR,  
637 Elliott KH. 2022. Accelerating animal energetics: High dive costs in a small seabird disrupt the  
638 dynamic body acceleration–energy expenditure relationship. *J Exp Biol.* 225: jeb243252. doi:  
639 10.1242/jeb.243252.
- 640 Tapper S, Nocera JJ, Burness G. 2020 Experimental evidence that hyperthermia limits offspring  
641 provisioning in a temperate- breeding bird. *R Soc Open Sci.* 7: 201589. doi: 10.1098/rsos.201589.
- 642 Torre-Bueno JR. 1976. Temperature regulation and heat dissipation during flight in birds. *J Exp Biol.* 65:  
643 471-482. doi: 10.1242/jeb.65.2.471.
- 644 Wada H, Cristol DA, McNabb FMA, Hopkins WA. 2009. Suppressed adrenocortical responses and thyroid  
645 hormone levels in birds near a mercury-contaminated river. *Environ Sci Technol.* 43: 6031-6038.  
646 doi: 10.1021/es803707f.
- 647 Williams CL, Ponganis PJ. 2021 Diving physiology of marine mammals and birds: the development of  
648 biologging techniques. *Phil Trans R Soc. B* 376: 20200211. doi: 10.1098/rstb.2020.0211.
- 649 Wilson RP, Pütz K, Grémillet D, Culik BM, Kierspel M, Regel J, Bost CA, Lage J, Cooper J. 1995.  
650 Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J*  
651 *Exp Biol.* 198: 1115–1135. doi: 10.1242/jeb.198.5.1115.
- 652 Wojczulanis-Jakubas K, Waż P, Jakubas D. 2020. Little auks under the midnight sun: diel activity rhythm  
653 of a small diving seabird during the Arctic summer. *Pol Res.* 39: 3309. doi:  
654 10.33265/polar.v39.3309.
- 655 Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of  
656 semiparametric generalized linear models. *J Roy Stat Soc B* 73: 3-36. doi: 10.1111/j.1467-  
657 9868.2010.00749.x.
- 658 Wood SN. 2017. *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman and  
659 Hall/CRC.