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1 **Keystone seabird may face thermoregulatory challenges in a warming Arctic**

2

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27 **Abstract**

28 Climate change affects the Arctic more than any other region, resulting in evolving weather, vanishing  
29 sea ice and altered biochemical cycling, which may increase biotic exposure to chemical pollution. We  
30 tested thermoregulatory impacts of these changes on the most abundant Arctic seabird, the little auk (*Alle  
31 alle*). This small diving species uses sea ice-habitats for foraging on zooplankton and resting. We  
32 equipped eight little auks with 3D accelerometers to monitor behavior, and ingested temperature recorders  
33 to measure body temperature ( $T_b$ ). We also recorded weather conditions, and collected blood to assess  
34 mercury (Hg) contamination. There were nonlinear relationships between time engaged in different  
35 behaviors and  $T_b$ .  $T_b$  increased on sea ice, following declines while foraging in polar waters, but changed  
36 little when birds were resting on water.  $T_b$  also increased when birds were flying, and decreased at the  
37 colony after being elevated during flight. Weather conditions, but not Hg contamination, also affected  $T_b$ .  
38 However, given our small sample size, further research regarding thermoregulatory effects of Hg is  
39 warranted. Results suggest that little auk  $T_b$  varies with behavior and weather conditions, and that loss of  
40 sea ice due to global warming may cause thermoregulatory and energetic challenges during foraging trips at  
41 sea.

42 **Keywords:** Body temperature; behavior; plasticity; environmental variation; climate change; biologging;  
43 activity patterns; dovekie

44  
45 **Introduction**

46 Global climate change is proceeding at unprecedented rates<sup>1</sup>, posing physiological and bioenergetic  
47 challenges for organisms<sup>2-4</sup>. Among direct effects of shifting weather regimes on animals,  
48 thermoregulatory challenges are particularly important<sup>5-9</sup>. Organisms are increasingly facing challenging  
49 thermal environments in the form of elevated temperatures, extreme heat events and stochasticity<sup>1</sup>. In  
50 addition, other environmental conditions, such as wind patterns and humidity affect heat exchange with  
51 the environment<sup>10,11</sup>, and may evolve under climate change<sup>1</sup>. Organisms are also facing shifts in resource  
52 distributions and changes in habitat structure, which may force changes in activity patterns and create

53 thermoregulatory challenges that disrupt energy balance. For example, modified vegetation structure may  
54 not only affect the resource base, but also limit availability of shade, and scope for behavioral  
55 thermoregulation<sup>12</sup>. Furthermore, in the Arctic, which is warming ~4 times faster than other regions<sup>1,13</sup>,  
56 advanced melting and decreased extent of sea ice may mean longer commutes to favorable foraging  
57 areas<sup>14</sup> and loss of an important resting substrate that provides thermal relief at sea<sup>15</sup>.

58 Compounding the challenges of climate change, organisms simultaneously face other environmental  
59 challenges, some of which are also linked to ecosystem engineering by humans. For example,  
60 anthropogenic activities have increased exposure to chemical contaminants, such as mercury<sup>16</sup>, and global  
61 warming has potential to exacerbate this threat<sup>17-19</sup>. Mercury (Hg) is a prevalent contaminant that reaches  
62 even remote polar regions via a repeated process of condensation and evaporation, persists in cold  
63 environments, and biomagnifies up marine food chains<sup>16,20,21</sup>. The methylated form, methylmercury  
64 (MeHg) is especially bioavailable and harmful to wildlife<sup>22</sup>. Exposure of animals to MeHg may be  
65 exacerbated by climate change<sup>23</sup>. For instance, conversion of inorganic Hg to MeHg is potentiated in  
66 warming oceans<sup>24</sup>. Hg contamination may interfere with body temperature ( $T_b$ ) regulation via endocrine  
67 disruption<sup>25</sup>, notably affecting production of thyroid hormones, which are central to thermoregulation<sup>26</sup>. In  
68 addition, Hg contamination could affect patterns of thermoregulation through effects on detoxification  
69 costs and resting metabolic rate<sup>27-29</sup>. Although few data specific to Hg are available, both hypo- and  
70 hyperthermic responses can occur in response to contamination<sup>30</sup>. Hypothermic responses are proposed to  
71 reflect an adaptive detoxification mechanism through which toxicity is reduced through facultative  
72 reduction in  $T_b$ <sup>30,31</sup>. Modification in  $T_b$  due to contaminant exposure could limit thermoregulatory  
73 adjustments in responses to global climate change, making it more difficult for animals to conserve water  
74 and energy.

75 In this study, we used a suite of advanced techniques to evaluate potential for shifting environmental  
76 conditions and Hg contamination to affect activity-specific  $T_b$  regulation in a keystone Arctic seabird, the  
77 little auk (or dovekie, *Alle alle*). We fit eight free-ranging birds with internal  $T_b$  loggers, which were  
78 ingested by focal individuals, and recorded abdominal temperature as a proxy of core  $T_b$  through time.

79 Birds were simultaneously equipped with miniaturized triaxial (3D) accelerometers that recorded body  
80 acceleration, allowing classification of activity budgets. We used data from an onsite weather station to  
81 gain insight into links between weather conditions and  $T_b$ . Finally, we obtained blood samples to assess  
82 whether Hg contamination could affect  $T_b$  and limit adaptive plasticity, although given our small sample  
83 size, we lack the power to draw strong conclusions regarding effects of Hg contamination.

84 We generated a suite of predictions based on our knowledge of the behavior, morphology and  
85 energetics of the little auk. In general, we predicted that environmental conditions and activity would  
86 interact to affect mean levels and variation in core  $T_b$ . More specifically, little auks have a high wing  
87 loading, resulting in extremely high energetic costs of flight<sup>32</sup>. Thus, we predicted that  $T_b$  would increase  
88 when birds were flying relative to during other activities, and that this increase would be magnified under  
89 conditions that reduce heat exchange between the body and environment or increase flight costs. In  
90 contrast, endothermic animals diving into cold polar waters face thermal challenge due to the high  
91 thermal conductance of water<sup>33,34</sup>. As a result, diving animals often allow  $T_b$  to fall below normothermic  
92 levels, which may facilitate aerobic dive capacity and limit energetic costs of heat loss to the  
93 environment<sup>34,35</sup>. Thus, we predicted that  $T_b$  would decline over the course of foraging episodes, and  
94 subsequently increase when birds were resting on sea ice. However, we recognized the potential that  
95 regional heterothermy, that is, variation in peripheral temperatures, especially in the appendages, might  
96 buffer changes in core  $T_b$  during diving, resulting in relative stability<sup>35</sup>. We also predicted that variation in  
97  $T_b$  might increase in the context of thermal challenge, which in the Arctic is most commonly experienced  
98 in the context of cold stress, especially during resting periods, but which could also involve heat stress,  
99 especially during activity. Finally, we predicted that higher blood Hg concentrations might affect  
100 thermoregulatory capacity. Thus, higher Hg concentrations could be linked to either higher mean  $T_b$ ,  
101 perhaps reflecting increased metabolic rates to support detoxification costs, or lower  $T_b$ , perhaps  
102 reflecting suppression of thyroid hormones. In addition, elevated blood Hg could be linked to greater  
103 variation in  $T_b$ , especially in the context of thermal stress. By adopting a multifaceted approach and

104 evaluating specific predictions, we grant insight into how thermoregulatory dynamics may shift given  
105 concomitant exposure to multiple environmental stressors.

106

## 107 **Materials and Methods**

108 **Study system:** Our study took place at a breeding population of little auks situated at Ukaleqarteq (Kap  
109 Höegh), East Greenland (70°44'N, 21°35'W). Little auks (~150 g) are the most abundant seabird in the  
110 high Arctic and breed in large colonies<sup>36</sup>. Both males and female incubate a single egg, and contribute  
111 equally to provisioning of the chick<sup>37,38</sup>. Little auks forage on copepods, and return to the colony from  
112 foraging sites at sea with prey items stored in a specialized gular pouch, which are then regurgitated for  
113 the chick<sup>38</sup>. Upon return to the colony, little auks can be captured and recaptured at or near the nesting  
114 sites in rock crevasses, facilitating fitting and retrieval of accelerometers and deployment of T<sub>b</sub> loggers.  
115 Mean blood Hg levels in little auks at Ukaleqarteq in recent years fall into the low risk range for  
116 toxicological effects. However, past research documents negative effects on reproduction<sup>39,40</sup> and body  
117 condition<sup>14</sup>, suggesting that despite relatively low Hg levels there may be other effects on physiology and  
118 thermoregulation. Fieldwork adhered to the ASAB/ABS guidelines for use of animals in behavioral  
119 research, and was conducted in accordance with Greenlandic law. The Government of Greenland,  
120 Ministry of Environment and Nature, and Department of Fisheries, Hunting and Agriculture, approved  
121 research procedures and provided ethical clearance (permit: 2020-1006). The methodology and results of  
122 this study are reported in accordance with ARRIVE guidelines.

123

124 **Deployment of T<sub>b</sub> loggers and accelerometers:** During July 2020, we captured eight little auks outside  
125 nesting crevasses using a combination of lassos and noose carpets. We fit each bird with a T<sub>b</sub> logger  
126 (BodyCap Anipill Core Body Temperature Ingestible Tablet; BMedical; ± 0.2°C; 1.7g; 17.7 × 8.9 mm;  
127 ~1% of mass), a data logging system for gastrointestinal temperature recording. These capsules are  
128 designed for use in birds, and have been used by a number of past studies on wild and free-ranging  
129 species<sup>41,42</sup>. Birds spontaneously ingested T<sub>b</sub> loggers placed within the beak. Loggers recorded abdominal

130 temperature every minute for periods of ca. 30h. We remotely downloaded data from loggers via  
131 telemetry when the bird was within ~1 m.  $T_b$  loggers are assumed to be eliminated through defecation or  
132 regurgitation, and are not recovered. Focal individuals were simultaneously equipped with miniaturized  
133 triaxial accelerometers (Axy 4, Technosmart, 3g, ~2% of mass), to record body acceleration. We attached  
134 accelerometers to the central breast at the level of the sternum using Tesa<sup>®</sup> tape. Accelerometers recorded  
135 data at a frequency of 50 Hz (50 readings per second). We marked birds with color rings to facilitate  
136 identification and recapture within ~4 days, upon which we retrieved the accelerometer. Deployment  
137 dates fell within nine days during the mid-late chick rearing phase [July 22-30]. All birds were breeding  
138 adults, but sex was not determined for this study, as the remaining volume of blood was conserved for  
139 other physiological assays. The thermoregulatory physiology of male and female little auks during the  
140 nestling stage is likely to be similar, as the sexes are monomorphic in coloration, overlap extensively in  
141 size (males may be slightly larger), and share equally in breeding duties<sup>37,38</sup>. Nevertheless, we recognize  
142 lack of knowledge of sex as a limitation to our work. A portable HOBO H21-USB weather station at the  
143 study site recorded weather conditions (every 1-min), including ambient temperature ( $T_a$ ; °C), relative  
144 humidity (RH; %) and wind speed ( $V$ ; m/s). Conditions measured at the weather station were taken as a  
145 proxy of environmental conditions at both the breeding site and at-sea foraging grounds (as a caveat, little  
146 auks can forage up to ~100 km from the colony<sup>43</sup>).

147

148 **Analysis of accelerometry and  $T_b$  data:** We used Igor Pro 8.04 (64-bit; WaveMetrics) to classify data on  
149 triaxial acceleration into behavioral states (see details in<sup>15</sup>). In brief, we used k-clustering analysis applied  
150 to acceleration axes, followed by application of a custom-written script, which utilized output from the  
151 clustering analysis and surface temperature data. Behavioral states identified were: flying, diving, on the  
152 water surface, on sea ice, and at the colony. We proceeded to determine whether time spent on the water  
153 was part of a foraging bout (i.e. inter-dive interval), or represented time resting on the water. To this end,  
154 we determined the dive bout ending criterion, using R package diveMove<sup>44</sup>, which applies the methods of  
155 <sup>45</sup> and <sup>46</sup> for identification of behavioral bouts. Using the standard method of classification, based on

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

164

165 **Mercury contamination: sampling and analysis:** We obtained ~0.2-0.5 ml blood samples from the  
166 brachial vein after recapture of birds to retrieve accelerometers, which minimized stress during the  
167 experimental period. Blood samples were centrifuged for 10 min at 3500 rpm to separate plasma from red  
168 blood cells (RBCs), which were stored in 70% ethanol. After evaporation of ethanol, RBCs were freeze  
169 dried for 48 hrs and homogenized prior to analysis for total Hg (hereafter Hg) concentrations. Total Hg  
170 serves as a proxy for highly toxic MeHg, since most of the Hg in bird blood, feathers and eggs is MeHg<sup>47</sup>.  
171 Samples were analyzed in duplicate using an Advanced Mercury Analyser spectrophotometer (Altec  
172 AMA 254) at the Institute Littoral Environnement et Sociétés (LIENSs)<sup>48</sup>. The standard deviation  
173 between duplicates was <10%. We used TORT-3 as a standardized reference material (CRM; Lobster  
174 Hepatopancreas Tort-3; NRC, Canada; [Hg] =  $0.292 \pm 0.022 \mu\text{g g}^{-1}$  dry weight (dw)) and performed a  
175 blank before initiating measurements on samples. The limit of detection for Hg and mean  $\pm$  SD of Tort-3  
176 measurements were  $0.005 \mu\text{g g}^{-1}$  dw and  $0.302 \pm 0.004 \mu\text{g g}^{-1}$  dw ( $N = 8$ ; replicates), respectively.

177

### 178 **Statistical analysis**

179 We conducted statistical analyses in R 3.6.1<sup>49</sup>. We used generalized additive mixed effect models  
180 (GAMMs) in R package mgcv<sup>50,51</sup> to assess whether  $T_b$  varied with behavior, environmental conditions,



181 or time of day. For this model, we used each observation of  $T_b$ . We used the corAR1 correlation structure  
182 in package nlme to account for temporal autocorrelation<sup>52</sup>, included individual ID and behavioral bout  
183 (nested within individual ID) as random effects, and incorporated two non-linear smooth terms. The first  
184 non-linear smooth term tested for non-linear variation between  $T_b$  and time in each behavioral state. To  
185 this end, we used a cubic regression spline (specified as `bs="cr"`) with the degree of smoothness set to  $k =$   
186 50 (which minimized AICc and increase the  $R^2$  relative to models with lower  $k$ ). We used the “by” call  
187 within the smoothing function to test for unique non-linear relationships within each behavioral state. For  
188 the second non-linear smooth term, we used a cyclic cubic regression spline (specified as `bs="cc"`) to test  
189 for variation in  $T_b$  with time of day. We also included two-way interactions between behavioral state and:  
190 (1)  $T_a$ , (2) RH, (3) wind speed, and (5) Hg concentrations. We removed interactions with P-values  $>$   
191 0.059 from models, followed by elimination of main effects above  $P > 0.05$ . We standardized continuous  
192 predictor variables to a mean of zero and standard deviation of one to facilitate interpretation of main  
193 effects when including interactions in models<sup>53</sup>. We used package emmeans<sup>54</sup> for pairwise comparisons  
194 between interaction terms (function `emtrends`) and differences in  $T_b$  between behavioral states (function  
195 `emmeans`).

196 To more thoroughly explore differences in how  $T_b$  changes with time when birds are engaged in  
197 different behaviors, we calculated change in  $T_b$  (deltas) for each behavioral bout as:  $\Delta T_b = T_{b,end} - T_{b,start}$ ;  
198 where  $T_{b,end} = T_b$  at the last time point recorded in that behavioral state and  $T_{b,start} = T_b$  at the first time  
199 point recorded. We used a linear mixed effects model in nlme to compare  $\Delta T_b$  across behavioral states,  
200 while including the length of the time interval in the model. We extracted and plotted predicted values  
201 from models using function `ggpredict` within the `ggeffects` package<sup>55</sup>. In addition, to evaluate modulators  
202 of the effect of time of day on  $T_b$ , we constructed GAMMs predicting  $T_a$  and RH from time of day, using  
203 the same random structure as above.

204 We also assessed whether between minute variation in  $T_b$  differed between behavioral states by  
205 calculating the absolute value of the difference between subsequent measurements of  $T_b$ , and constructing

206 models with the same structure described for mean  $T_b$ . Values could not be calculated for time points at  
207 the beginning of behavioral intervals, so these rows were dropped from the analysis.

208

## 209 **Results**

210 **Predictors of little auk  $T_b$  across behavioral states:** Mean  $\pm$  SD  $T_b$  of little auks was  $41.0 \pm 0.55^\circ\text{C}$  and  
211 showed significant, but low magnitude differences between behaviors (Table 1; see Table S1 for full  
212 GAMM, including non-significant effects). Estimated marginal means (EMM  $\pm$  SE [95% CI]) for  $T_b$  were  
213 significantly lower for diving ( $40.7 \pm 0.092$  [40.5, 40.8]  $^\circ\text{C}$ ) relative to in other behaviors ( $P < 0.001$  in all  
214 cases; Table S1 for pairwise comparisons), but did not differ between flying ( $41.55 \pm 0.092$  [41.4, 41.7]  
215  $^\circ\text{C}$ ), at the colony ( $41.4 \pm 0.089$  [41.2, 41.6]  $^\circ\text{C}$ ), on sea ice ( $41.4 \pm 0.088$  [41.2, 41.6]  $^\circ\text{C}$ ), or on the water  
216 ( $41.4 \pm 0.105$  [41.2, 41.6]  $^\circ\text{C}$ ) (Table S2 for pairwise comparisons).

217 The minimum adequate model predicting  $T_b$  included non-linear relationships with time spent in each  
218 of the behaviors, with the exception of time spent on the water surface, for which the relationship was  
219 non-significant (Table 1).  $T_b$  decreased with the amount of time spent diving up to  $\sim 19$  minutes, from  
220  $\sim 41.5$  to  $40.6^\circ\text{C}$ , after which predicted  $T_b$  plateaued (Fig. 1a). There was also a more gradual decrease in  
221  $T_b$  after birds arrived at the colony up to  $\sim 90$  min, from  $41.9$  to  $40.9^\circ\text{C}$  (Fig. 1a). On the other hand,  $T_b$   
222 increased the longer birds spent flying to  $\sim 15$  minutes, from  $\sim 41.3$  to  $41.6^\circ\text{C}$ , before leveling off or  
223 declining slightly (Fig. 1a).  $T_b$  also displayed an increase for the initial 30 minutes when birds were on the  
224 sea ice, from  $\sim 40.8$  to  $41.4^\circ\text{C}$ , after which  $T_b$  leveled off or declined slightly (Fig. 1a). Figure 2 shows a  
225 trace of  $T_b$  through time for one focal individual. See Fig. S1-S7 for other birds.

226 The overall  $\Delta T_b$  for diving was negative, with the 95% CI not overlapping zero (EMM  $\pm$  SE [95% CI]  
227 =  $-0.312 \pm 0.026$  [-0.374, -0.251]  $^\circ\text{C}$ ), and was lower than all other  $\Delta T_b$  (Table S3 for pairwise  
228 comparisons). The  $\Delta T_b$  for flying and on sea ice were positive, with CIs not overlapping zero (EMM  $\pm$  SE  
229 [95% CI] =  $0.146 \pm 0.029$  [0.077, 0.215]  $^\circ\text{C}$ ;  $0.335 \pm 0.045$  [0.228, 0.443]  $^\circ\text{C}$ ), and were higher than all  
230 other  $\Delta T_b$ , with  $\Delta T_b$  for sea ice also greater than that of flying (Table S3 for pairwise comparisons). The

231 overall  $\Delta T_b$  for at the colony and on the water were negative, and positive, respectively, but did not  
 232 significantly differ from each other or zero (Estimate marginal mean  $\pm$  SE =  $-0.074 \pm 0.044$  [-0.179,  
 233  $0.031$ ] °C;  $0.0002 \pm 0.038$  [-0.089, 0.089] °C, respectively).

234

235 **Table 1.** Minimum adequate GAMM for body temperature ( $T_b$ ; °C) in little auks as a function of  
 236 behavioral state, weather conditions, and time.

<i>Parametric coefficients</i>					
<b>Variables</b>	<b><math>\beta \pm SE</math></b>	<b><i>t</i></b>	<b><i>P</i>&gt;( <i>t</i> )</b>	<b><i>F</i></b>	<b><i>P</i>(&gt;<i>F</i>)</b>
Intercept	40.6 $\pm$ 0.464	87.414	< 0.001		
Flying <sup>a</sup>	0.922 $\pm$ 0.496	1.857	0.063	7.271	<0.001
Colony	0.817 $\pm$ 0.462	1.767	0.077		
Ice	0.325 $\pm$ 0.469	0.692	0.489		
Water	0.686 $\pm$ 0.495	1.385	0.166		
Wind speed (m/s)	-0.016 $\pm$ 0.007	-2.407	0.016	5.792	0.016
Relative humidity (%)	0.063 $\pm$ 0.013	5.028	<0.001	25.3	<0.001
Flying $\times$ wind	0.028 $\pm$ 0.010	2.836	0.004	2.345	0.052
Colony $\times$ wind	0.020 $\pm$ 0.010	2.012	0.044		
Ice $\times$ wind	0.021 $\pm$ 0.010	2.167	0.030		
Water $\times$ wind	0.016 $\pm$ 0.011	1.405	0.159		
<i>Approximate significance, Smoothed terms</i>					
	<b><i>edf</i></b>	<b><i>Ref.df</i></b>	<b><i>F</i></b>	<b><i>P</i>(&gt;<i>F</i>)</b>	
s(Time behavior): Diving	9.434	9.434	67.2	<0.001	
s(Time behavior): Flying	5.991	5.991	10.1	<0.001	
s(Time in behavior): Colony	5.933	5.933	22.5	<0.001	
s(Time in behavior): Ice	5.097	5.097	21.2	<0.001	
s(Time in behavior): Water	2.110	2.110	0.738	0.446	
s(Time of day)	6.467	18.0	3.940	<0.001	
<b>R-adjusted</b>	0.212	<b>N</b>	16405, 8		

237 <sup>a</sup>Relative to diving

238

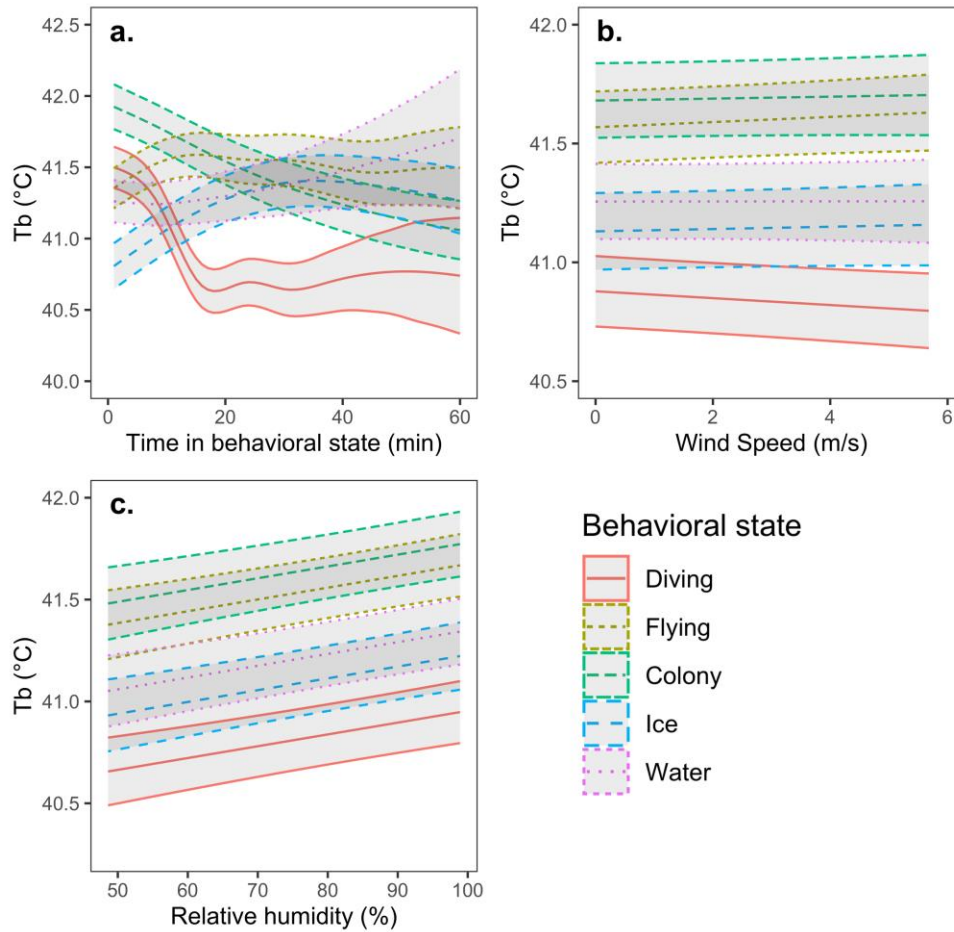
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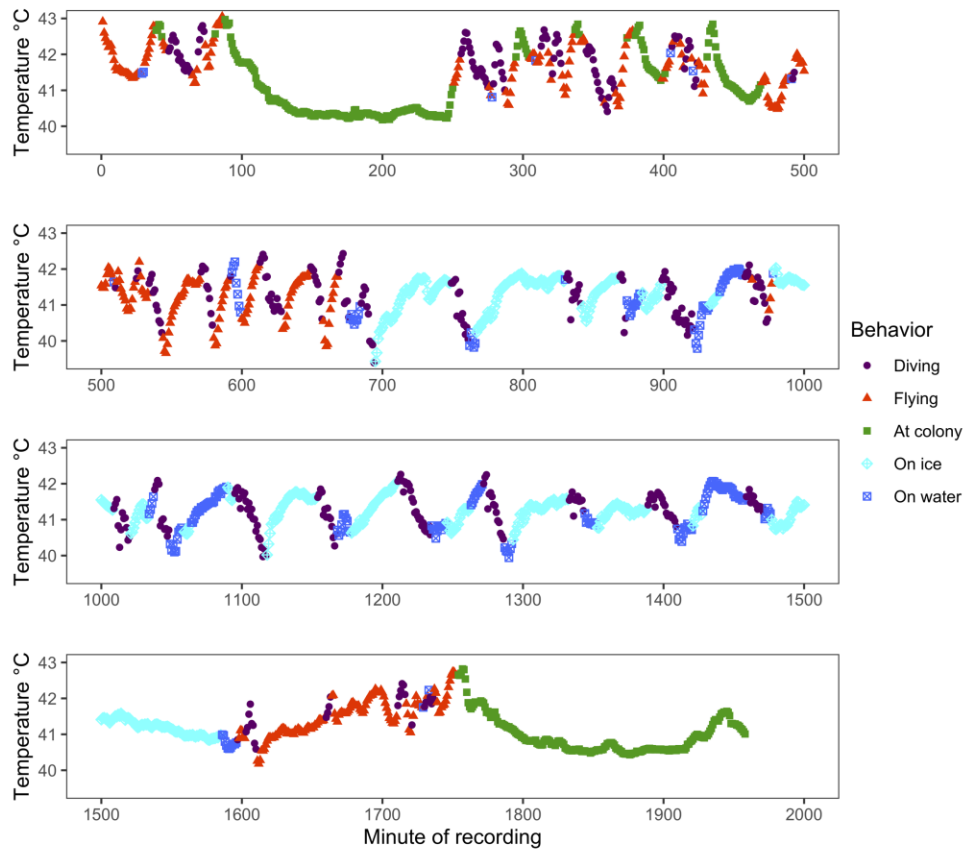
244

245 **Figure 1.** Relationships between  $T_b$  ( $^{\circ}\text{C}$ ) of little auks predicted from the GAMM and (a) time within the  
 246 behavioral state (min), (b) wind speed (m/s), and (c) Relative humidity (%). Shaded regions show 95%  
 247 CIs.

248

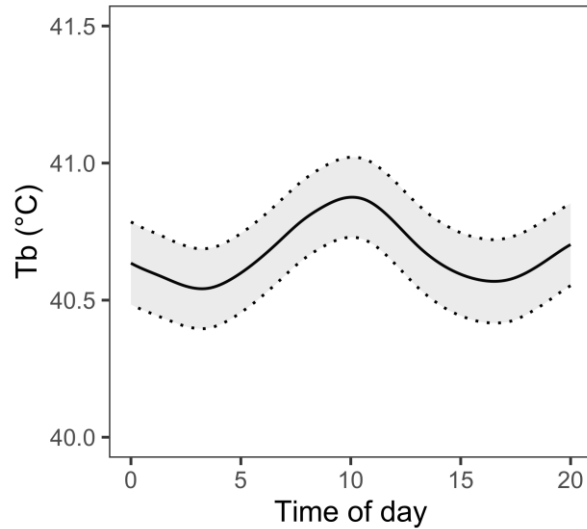
249 With respect to environmental effects, there was a significant interaction between behavioral state and  
 250 wind speed in predicting  $T_b$  (Table 1).  $T_b$  tended to increase with wind speed when birds were flying, but  
 251 not in other behavioral states (Table 1; Fig. 1b; Table S4 for pairwise comparisons). In addition,  $T_b$  was  
 252 positively related to RH (Table 1; Fig. 1c), independent of behavioral state (Table S1).  $T_a$  was unrelated  
 253 to  $T_b$ , either independently, or in interaction with behavioral state (Table S1).

254



255  
 256 **Figure 2.** Body temperature ( $T_b$ ) through time color coded with respect to behavioral state for one little  
 257 auk (LIAK20EG19) from the Ukaleqarteq, East Greenland, population. Note rebounds in  $T_b$  when on sea  
 258 ice following declines while diving in cold Arctic waters.  $T_b$  also generally increases with time flying and  
 259 declines with time at the colony.

260  
 261 Finally, the best model predicting  $T_b$  included a non-linear effect of time of day on  $T_b$  (Table 1; Fig. 3),  
 262 with bimodal peaks in the late morning (~10:00) and around 20:00, and the lowest values in the early  
 263 morning (~4:00 am) and around 16:00 (Fig. 3). When examining potential environmental effects  
 264 underlying this relationship, we found that there was a non-linear, but unimodal, relationship between  
 265 time of day and  $T_a$ , with a peak around ~16:00 (edf = 7.33,  $F_8 = 175$ ,  $P < 0.001$ ; Fig. S8). Similarly, RH  
 266 was non-linearly related to time, and showed a reverse pattern to  $T_a$ , with a nadir around ~16:00 (edf =  
 267 7.30,  $F_8 = 203$ ,  $P < 0.001$ ; Fig. S9).



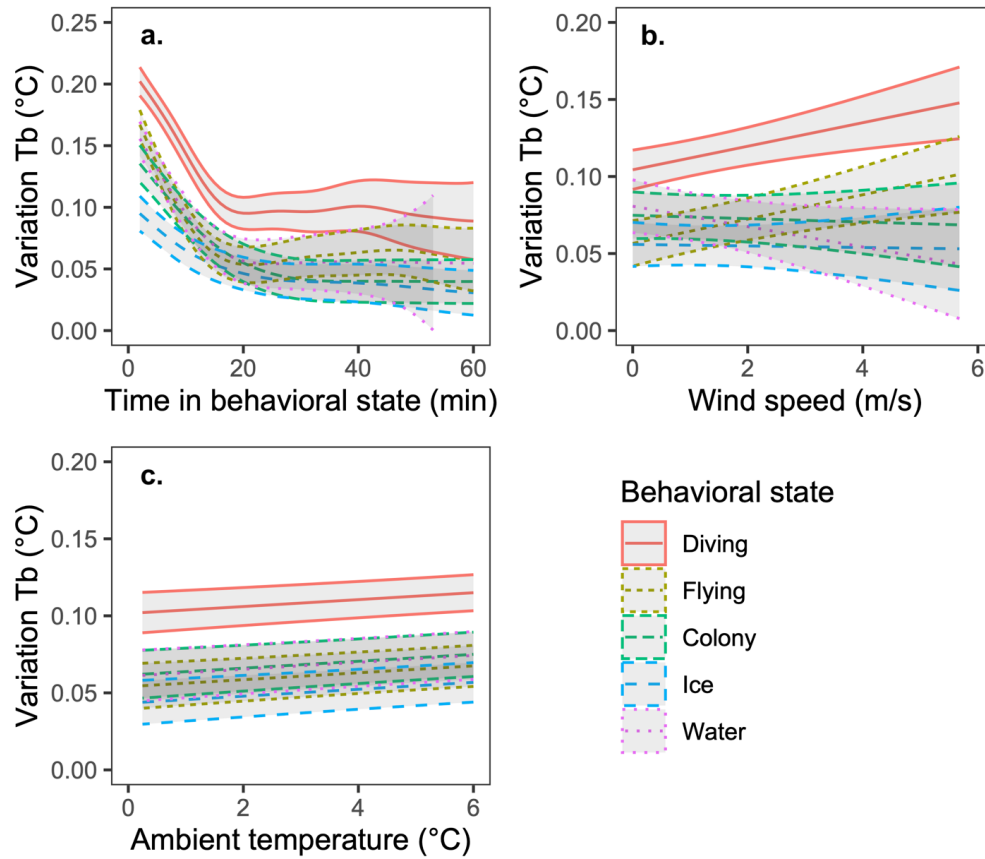
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269 **Figure 3.** Relationship between  $T_b$  (°C) of little auks predicted from the GAMM and time of day. Shaded  
 270 regions show 95% Cis.

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272 **Predictors of between minute variation in  $T_b$ :** Mean  $\pm$  SD between minute variation in  $T_b$  ( $|T_{b1}-T_{b1+1}|$ )  
 273 of little auks was  $0.09 \pm 0.11^\circ\text{C}$  (range: 0-1.5 °C), and showed low magnitude, significant variation  
 274 between behavioral states (Table 2; Table S5 for full model). The EMM ( $\pm$  SE) was highest when birds  
 275 were foraging at sea ( $0.097 \pm 0.008$  [0.080, 0.113] °C), followed by flying ( $0.060 \pm 0.008$  [0.044, 0.077]  
 276 °C), on the water ( $0.055 \pm 0.011$  [0.033, 0.078] °C), at the colony ( $0.041 \pm 0.008$  [0.024, 0.057] °C) and  
 277 on sea ice ( $0.040 \pm 0.007$  [0.025, 0.054] °C), but the only significant differences were between diving and  
 278 all other behavioral states (Table S6 for pairwise contrasts). There were significant non-linear  
 279 relationships between time in the behavioral state and between minute variation in  $T_b$  (Table 2); which  
 280 involved early decreases with time in the behavioral state for all behaviors, before leveling off (Fig. 4a).  
 281 This decrease was steepest when birds were resting on the water, diving, or in flight (all with a slope of  $\sim$   
 282  $-0.007^\circ\text{C min}^{-1}$  in the first  $\sim 15$  min), and slightly more gradual at the colony (slope of  $\sim -0.004^\circ\text{C min}^{-1}$  in  
 283 the first  $\sim 25$  min) and on the sea ice (slope of  $\sim -0.002$  in the first  $\sim 15$  min) (Fig. 4a).

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**Figure 4.** Between minute variation in little auk body temperature ( $|T_{b_i} - T_{b_{i+1}}|$ ) (°C) in different behavioral states as a function of a) time in behavioral state, b) wind speed, and c) ambient temperature (°C). Plots show predicted values from GAMMs, with shaded regions representing 95% CIs.

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With respect to environmental effects, there was an interaction between wind speed and behavioral state in predicting between minute variation in  $T_b$  (Table 2; Fig. 4b). Variation in  $T_b$  increased with wind speed when birds were diving and flying but did not vary significantly with wind speed in the other behavioral states (Table S7 for pairwise comparisons). There was a positive correlation between  $T_a$  and variation in  $T_b$  (Table 2; Fig. 4c) independent of behavioral state (Table S5). When  $T_a$  was also in the model, RH was unrelated to variation in  $T_b$  (Table S5). However, when  $T_a$  was removed, RH was negatively related to variation in  $T_b$  ( $\beta \pm SE = -0.006 \pm 0.002$ ,  $T = -3.42$ ,  $P = 0.006$ ), independent of behavioral state (Table S5).

300 Between minute variation in  $T_b$  did not vary with time of day (Table S5).

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302 **Table 2.** Minimum adequate GAMM predicting between minute variation in body temperature ( $T_{b1}$ -  
303  $T_{b1+1}$ ) ( $^{\circ}\text{C}$ ) in little auks as a function of behavioral state and weather conditions.

<i>Parametric coefficients</i>					
<b>Variable</b>	$\beta \pm \text{SE}$	<i>t</i> -value	<i>P</i> (>   <i>t</i>  )	<i>F</i>	<i>P</i> (> <b>F</b> )
Intercept	0.155 ± 0.036	4.240	< 0.001		
Flying	-0.039 ± 0.053	-0.727	0.467	1.701	0.147
Colony	-0.076 ± 0.037	-2.069	0.039		
Ice	-0.090 ± 0.038	-2.366	0.018		
Water	-0.067 ± 0.081	-0.821	0.412		
Wind speed (m/s)	0.008 ± 0.002	3.372	0.001	11.373	< 0.001
Temperature ( $^{\circ}\text{C}$ )	0.006 ± 0.002	3.882	< 0.001	15.074	< 0.001
Flying × wind	0.0002 ± 0.004	0.077	0.939	5.023	< 0.001
Colony × wind	-0.010 ± 0.004	-2.598	0.009		
Ice × wind	-0.010 ± 0.004	-2.317	0.021		
Water × wind	-0.016 ± 0.005	-3.415	< 0.001		
<i>Approximate significance, Smoothed terms</i>					
	<i>edf</i>	<i>Ref.edf</i>	<i>F</i>	<i>P</i> (> <b>F</b> )	
s(Time behavior):Diving	6.315	6.315	66.68	< 0.001	
s(Time behavior):Flying	6.688	6.688	50.26	< 0.001	
s(Time behavior):Colony	11.58	11.58	15.75	< 0.001	
s(Time behavior):Ice	5.150	5.150	16.97	< 0.001	
s(Time behavior):Water	3.348	3.348	40.46	< 0.001	
<b>R<sup>2</sup>-adjusted</b>	0.234	<b>N</b>	15136, 8		

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305 **Mercury contamination:** There was no significant relationship between Hg contamination and  $T_b$  (Table  
306 S1) or between minute variation in  $T_b$  (Table S5). The mean ± SE of Hg concentrations in RBCs was  
307  $1.290 \pm 0.031 \mu\text{g g}^{-1} \text{ dw}$  [range:  $1.030$ - $1.746 \mu\text{g g}^{-1} \text{ dw}$ ], which assuming 79% blood moisture content is  
308 equivalent to  $0.271 \pm 0.007 \mu\text{g g}^{-1} \text{ ww}$  [range:  $0.216$ - $0.367 \mu\text{g g}^{-1} \text{ ww}$ ], and falls within the low risk range  
309 for toxicological effects ( $0.2$ – $1.0 \mu\text{g g}^{-1} \text{ ww}^{47}$ ; calculated for whole blood, but comparable to levels in  
310 RBCs). Table 3 lists the Hg concentrations in RBC of each focal bird in dw and ww equivalents.

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315 **Table 3.** Hg concentrations  $\mu\text{g g}^{-1}$  in dw and ww measured in the RBCs of focal birds breeding at  
316 Ukaleqarteq, East Greenland.

Focal individual	[Hg] $\mu\text{g g}^{-1}$ dw, ww
LIAK20EG09	1.030, 0.216
LIAK20EG12	1.350, 0.284
LIAK20EG14	1.038, 0.218
LIAK20EG17	1.334, 0.280
LIAK20EG19	1.216, 0.255
LIAK20EG24	1.075, 0.226
LIAK20EG25	1.746, 0.366
LIAK20EG28	1.527, 0.321

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### 318 **Discussion**

319 By employing advanced biologging approaches, we demonstrate that the  $T_b$  of a free-ranging seabird is  
320 sensitive to variation in activity patterns and environmental conditions, and suggest thermoregulatory  
321 challenges that may arise under climate change scenarios. In particular, results suggest that the evolving  
322 nature of the Arctic cryosphere, especially sea ice extent and coverage, may not only alter foraging  
323 conditions for little auks<sup>14,56,57</sup>, but also affect thermoregulatory dynamics during foraging trips at sea.  
324 There was no evidence that Hg contamination modifies the  $T_b$  of little auks, but our results regarding  
325 potential toxicological effects on thermoregulatory capacity are limited by a small sample size. Thus,  
326 further research is called for in this area.

327 Changes in  $T_b$  with activity were generally as expected.  $T_b$  declined while little auks were foraging in  
328 cold waters. This decline may facilitate aerobic capacity and limit heat loss, but also reflects  
329 thermoregulatory challenge<sup>34,58,59</sup>. In addition, declines in  $T_b$  while foraging, and high variability in  $T_b$ ,  
330 may arise from ingestion of cold prey. Indeed, ingestion-linked declines in  $T_b$  have been used to identify  
331 feeding events<sup>60</sup>, but our data lacked resolution to achieve this end. In another Alcid, Brünnich's  
332 guillemots (*Uria lomvia*),  $T_b$  declined over sequential diving bouts<sup>35</sup>. However, this decline occurred

333 during periods of resting on the water. During dives themselves,  $T_b$  increased and the peripheral  
334 temperature declined<sup>35</sup>. This pattern contrasts to  $T_b$  declines during diving observed in some penguin  
335 species<sup>59,61,62</sup>, and may reflect peripheral vasoconstriction and high wing beat frequency that generates  
336 heat<sup>35</sup>. Our data could not separate changes in  $T_b$  during dives and inter-dive intervals. Thus, a similar  
337 dynamic could be occurring in little auks.

338 Also as expected,  $T_b$  was highest when little auks were flying although the estimated marginal mean  
339 was not significantly different than when birds were on sea ice, at the colony, or on the water.  
340 Furthermore,  $T_b$  increased during flight before leveling off, reflecting heat generated by intense physical  
341 activity. Indeed, little auks have high wing loadings and flight costs ( $\sim 7.24 \times \text{BMR}^{32}$ ), which is expected  
342 to generate substantial amounts of heat and elevate  $T_b$ .

343  $T_b$  was also high when little auks arrived at the colony.  $T_b$  then declined before leveling off. This  
344 decrease in  $T_b$  may reflect decreases following commuting flights between foraging sites and the colony,  
345 with a decline in diet-induced thermogenesis (i.e. heat production associated with digestion, also referred  
346 to as specific dynamic action<sup>63</sup>), also potentially contributing.  $T_b$  of little auks at the colony was also  
347 relatively invariable, which could suggest that the colony serves as a thermal refuge for little auks. During  
348 the current study, we did not detect evidence that little auks were subject to thermal stress on land. The  
349 upper critical temperature (UCT) of little auks is  $\sim 20^\circ\text{C}^{64}$ , a temperature not reached during the relatively  
350 cool 2020 breeding season. However, an air temperature of  $20^\circ\text{C}$  was exceeded twice during July 2021,  
351 and captured birds were observed to rapidly exhibit sign of overheating (*unpublished data*). The operative  
352 temperature of little auks may be further elevated by solar radiation off the rocks, especially given their  
353 black plumage coloration<sup>9</sup>. Thus, with ongoing climate change, heat stress at the colony may eventually  
354 pose a threat, especially in the context of stress from predation pressure, which can activate flight-fight  
355 responses, or social interactions, which have been shown to elevate  $T_b$  in a range of animal species<sup>65-67</sup>.  
356 Indeed, due to their Arctic habitat and amphibious live style, little auks have evolved a low thermal  
357 conductance, which conserves heat and energy under cold conditions, but creates a challenge for heat  
358 dissipation<sup>64</sup>.

359 As predicted, little auks'  $T_b$  increased substantially on sea ice following declines during diving  
360 episodes, before leveling off, suggesting that loss of sea ice as a resting substrate may elevate  
361 thermoregulatory costs, negatively affecting energy balance.  $T_b$  was initially low when little auks first  
362 emerged on the sea ice, which could reflect that birds exit the water when  $T_b$  falls below a threshold,  
363 triggering birds to cease foraging activity<sup>35</sup>. For the first 30 minutes,  $T_b$  on sea ice increased by an average  
364 of ca.  $0.02^\circ\text{C min}^{-1}$ , while during foraging  $T_b$  dropped by an average of ca.  $-0.05^\circ\text{C min}^{-1}$  for the first 19  
365 minutes. Thus, the rate of  $T_b$  loss while foraging was greater than the rate of gain on ice, but given that the  
366 average ice bout lasted ca. 25 min and the average foraging bout ca. 9 min, time spent on ice would allow  
367 for recovery of  $T_b$ . On the other hand, there was no significant relationship between time resting on the  
368 water and  $T_b$ , and although positive, the  $\Delta T_b$  of birds resting on water surface was not significantly  
369 different than zero, suggesting little potential for recovery of  $T_b$  after foraging bouts. Furthermore, the  
370 lowest variation in  $T_b$  occurred when birds were on sea ice, and the highest during diving behavior,  
371 suggesting that resting on sea ice plays an important role in allowing birds to restore and maintain  
372 normothermic temperatures after thermally challenging foraging bouts.

373 In the context of climate change, sea ice loss may have energetic and thermoregulatory implications, as  
374 birds are forced to instead rest on the water, which has  $\sim 25 \times$  higher thermal conductivity than air<sup>33,68</sup>. In  
375 auks, compression of air space in feathers while diving reduces insulative properties, further facilitating  
376 heat exchange with the environment<sup>69</sup>. The costs of resting both in the air and on the water may be  
377 reduced by warming temperatures<sup>70</sup>. However, the thermal neutral zone, outside of which metabolic rate  
378 must be elevated to maintain  $T_b$ , has been shown to be considerably narrower for seabirds resting on the  
379 water relative to when resting in air, with metabolic rate also increasing more steeply below the lower  
380 critical temperature (LCT) in some species<sup>71</sup>. For example, in Brünnich's guillemot, the LCT in air and  
381 water are 2 and  $16^\circ\text{C}$ , respectively<sup>71,72</sup>, and the rate of increase in metabolic rate below the LCT is  
382 substantially greater in water than in air ( $0.60$  versus  $0.17 \text{ W} \times \text{kg}^{-1} \text{ }^\circ\text{C}^{-1}$ )<sup>71</sup>. Similarly, in another small  
383 diving seabird, the Cassin's auklet (*Ptychoramphus aleuticus*), the LCT in air and water were 16 and

384 21°C, respectively, and resting metabolic rate was 25% higher in water than in air<sup>73</sup>. Although,  
385 comparable data for the little auk is unavailable, these species are in the same family (Alcidae) as the little  
386 auk, and share a similar ecology.

387 At the Ukaleqarteq study site, even in an exceptionally warm year (2021) with very low sea ice  
388 coverage (mean  $\pm$  SE: 0.04  $\pm$  0.02 %), sea surface temperature within the foraging range (mean  $\pm$  SE:  
389 5.89  $\pm$  0.38 °C)<sup>15</sup> remained well below the LCTs in water reported for other Alcids (see above). Thus,  
390 even in warming oceans, little auks resting on the water may need to elevate their metabolic rate relative  
391 to when resting on ice, which, *in lieu* of compensatory changes, could elevate daily energy expenditure<sup>74</sup>,  
392 induce birds to return to the colony sooner, limiting time for energy acquisition, or force higher feeding  
393 rates. In addition, we recently demonstrated that high SST is associated with elevated daily energy  
394 expenditure in Ukaleqarteq little auks, a phenomenon associated with increased flight costs, as birds  
395 appeared to fly further to reach foraging grounds<sup>75</sup>. Longer flights may be motivated by the higher quality  
396 of lipid-rich copepods associated with colder ocean temperatures, but also by the opportunity to use sea  
397 ice as a resting substrate<sup>15,75</sup>. Loss of sea ice as a substrate for resting, foraging, and movement has  
398 demonstrated effects on energy balance in many sea ice-dependent species<sup>76-78</sup>. For instance, polar bears  
399 (*Ursus maritimus*) and narwhal (*Monodon monoceros*) show 3-4 fold increases in locomotory costs in  
400 association with sea ice declines<sup>78</sup>.

401  $T_b$  of little auks was also sensitive to environmental conditions. However, mean  $T_b$  was not related to  
402  $T_a$ . It is possible that a non-linear relationship could exist between  $T_a$  and  $T_b$ , which we could not capture  
403 given our modeling approach. On the other hand, variation in  $T_b$  increased with  $T_a$  across behavioral  
404 states, which could indicate that these cold-adapted birds face increasing challenges maintaining stable  $T_b$   
405 at higher temperatures, although, again, ambient temperature did not exceed the UCT of little auks in this  
406 study.  $T_b$  also increased with RH across behavioral states. As RH rises, capacity for evaporative heat  
407 dissipation decreases, resulting in increases in  $T_b$  or elevated thermoregulatory costs to maintain optimal  
408  $T_b$ <sup>79,80</sup>. In contrast,  $T_b$  tended to increase with wind speed when birds were in flight and decreased with

409 wind speed when birds were diving. High winds have been associated with increased energetic costs of  
410 flight for many avian species with a flapping flight mode<sup>81</sup>, whereas  $T_b$  while foraging in cold waters  
411 could be further reduced by high winds via enhanced thermal conductance and heat loss. As for mean  $T_b$ ,  
412 wind speed and behavioral state interacted to predict between minute variation in  $T_b$ . Specifically,  
413 between minute variation in  $T_b$  increased with wind speed when birds were flying and diving, while  
414 varying little with wind speed in the other behavioral states. A possible explanation for these results is  
415 that little auks have difficulty maintaining thermal stability when foraging in turbulent seas and flying in  
416 challenging conditions induced by higher winds. In the context of climate change, results suggest that  
417 alterations in RH and  $T_a$  may have implications for  $T_b$  regulation that are independent of behavioral state.  
418 On the other hand, changes in wind patterns may have especially high costs during active periods, with  
419 increases in storm events associated with climate change potentially elevating energy expenditure. As a  
420 caveat, weather conditions measured at the colony were taken as a proxy of conditions experienced by  
421 birds across behavioral states. Thus, given that little auks can forage up to ~100 km from the colony,  
422 results regarding effects of weather conditions on  $T_b$  should be interpreted with caution. Unfortunately,  
423 we did not have access to off-shore weather data on a fine temporal scale, and since birds were not GPS-  
424 tracked, we also had no way of knowing their precise locations during foraging trips.

425 We found no evidence for a relationship between Hg contamination and  $T_b$ . However, our effective  
426 sample size for testing the relationship was low. In addition, little auks have lower Hg levels than many  
427 seabirds species that feed at higher trophic levels. Thus, our results regarding the relationship between Hg  
428 contamination and  $T_b$  are preliminary, and further research is needed in this area, perhaps utilizing a  
429 different species with higher contamination levels. To our knowledge, there is currently no study  
430 documenting a link between Hg concentrations and  $T_b$  in free-ranging animals. However, laboratory  
431 studies have demonstrated hypothermic responses to Hg exposure, for instance, in the mouse (*Mus*  
432 *musculus*)<sup>82</sup>. Hypothermic responses to contamination are hypothesized to reduce the toxicity of the  
433 chemical in the body<sup>30</sup>, but could create challenges for survival in dynamic thermal environments. We

434 also observed weak, non-significant negative relationships between Hg levels and variation in  $T_b$ , which  
435 is inconsistent with the hypothesis that contaminated birds have more difficulty maintaining stable  $T_b$ .

436 Finally, there was a non-linear, bimodal relationship between time of day and  $T_b$ . The highest values  
437 occurred in late morning and at night and the lowest in early morning and late afternoon. The pattern in  $T_b$   
438 observed did not parallel daily cyclicality in  $T_a$  and RH, suggesting that it cannot be explained solely by  
439 diel variation in weather patterns. However, despite the fact that little auks in our population breed under  
440 24-hrs of daylight, the pattern may reflect a combination of the timing of maximum solar radiation  
441 exposure, diel activity patterns, and/or underlying circadian rhythmicity in  $T_b$  independent of activity. A  
442 past study on little auks found a regular rhythm of population attendance at the population level, perhaps  
443 linked to variation in predation pressure, which provides some foundation for expecting that  $T_b$  could also  
444 display cyclic variation. However, this same study found little circadian rhythm in activity of individual  
445 little auks<sup>83</sup>. In contrast to mean  $T_b$ , between minute variation in  $T_b$  did not correlate with time of day.

446 **Conclusions:**  $T_b$  of little auks fluctuated according to behavioral state and environmental conditions,  
447 which likely aids animals in optimizing energy balance while performing essential behaviors in complex  
448 environments. Although this plasticity is predicted to facilitate energy balance in the face of climate  
449 change, the dynamic nature of  $T_b$  regulation also suggests that changing environmental conditions may  
450 significantly alter energy balance, or the behavioral and energetic strategies that must be adopted to  
451 achieve energetic homeostasis. Our data suggests that little auks use sea ice as a thermal refuge, resting on  
452 this substrate to allow  $T_b$  to rebound after submersion in cold water and ingestion of cold prey items. If  
453 sea ice decreases due to warming temperature, thermoregulatory costs are forecast to increase as birds are  
454 instead required to rest on the water surface, which may force restructuring of foraging strategies. No  
455 relationship was found between  $T_b$  of little auks and Hg concentrations, but our results are preliminary,  
456 and we call for more research on the effects of chemical contaminations on  $T_b$ , especially in interaction  
457 with other environmental stressors.

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459

460 **Data availability:**

461 The datasets generated during the current study are publicly available via the Zenodo community of  
462 European Commission Funded Research (OpenAIRE) online data repository  
463 (<http://doi.org/10.5281/zenodo.7220883>).

464

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