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

3
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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 ~ 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[®] tape adhered to the feathers. We marked birds with color rings to
138 facilitate identification and recapture within ~ 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 `emtrends` 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 (ΔT_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 ΔT_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 ± 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.

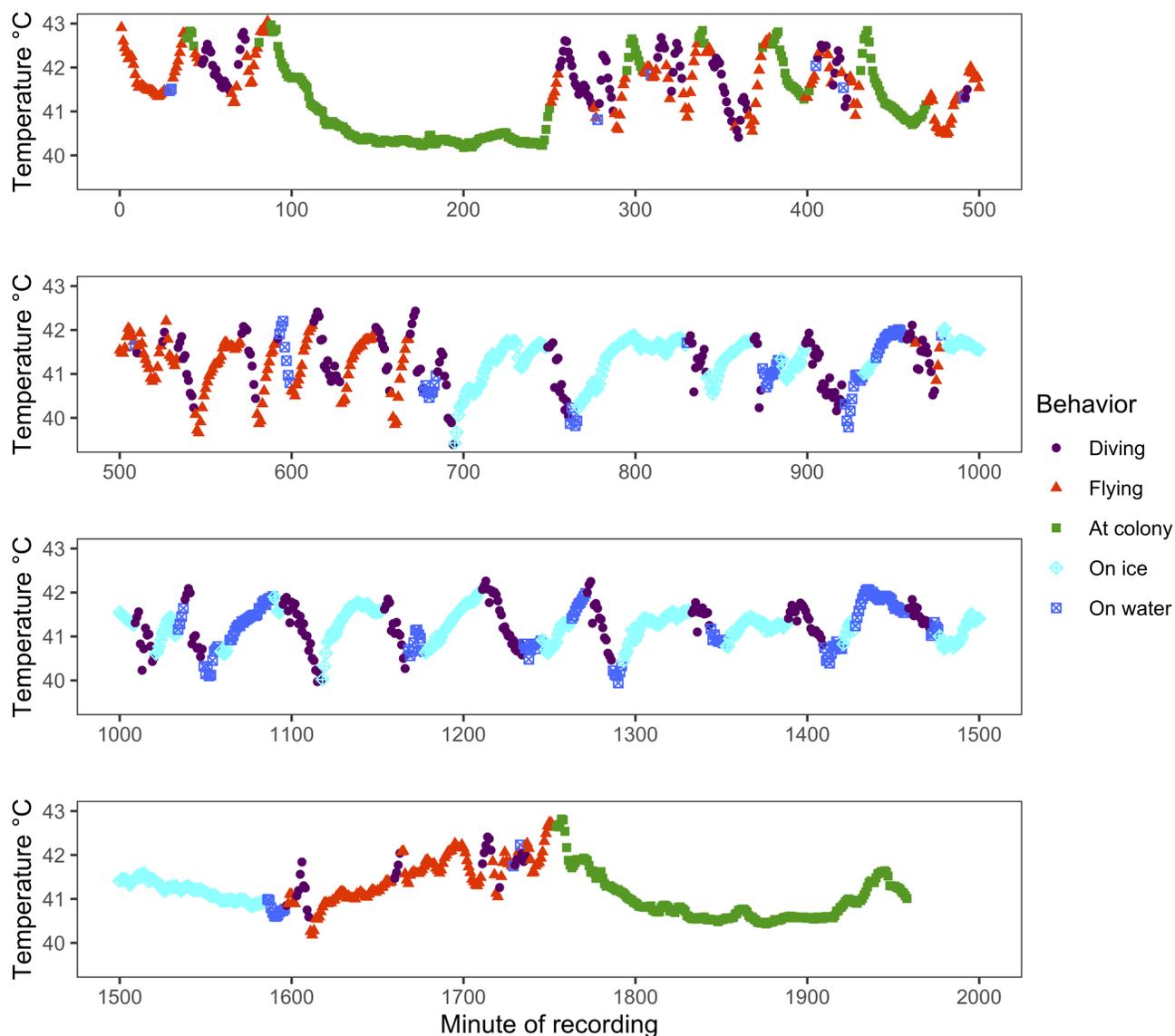
215
 216 **Table 1.** Differences in mean T_b of little auks in the five behavioral states: (a) estimated marginal (EM)
 217 means from the best-fitting GAMM with interactions removed (df = 16391), (b) pairwise contrasts
 218 between behavioral states.

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

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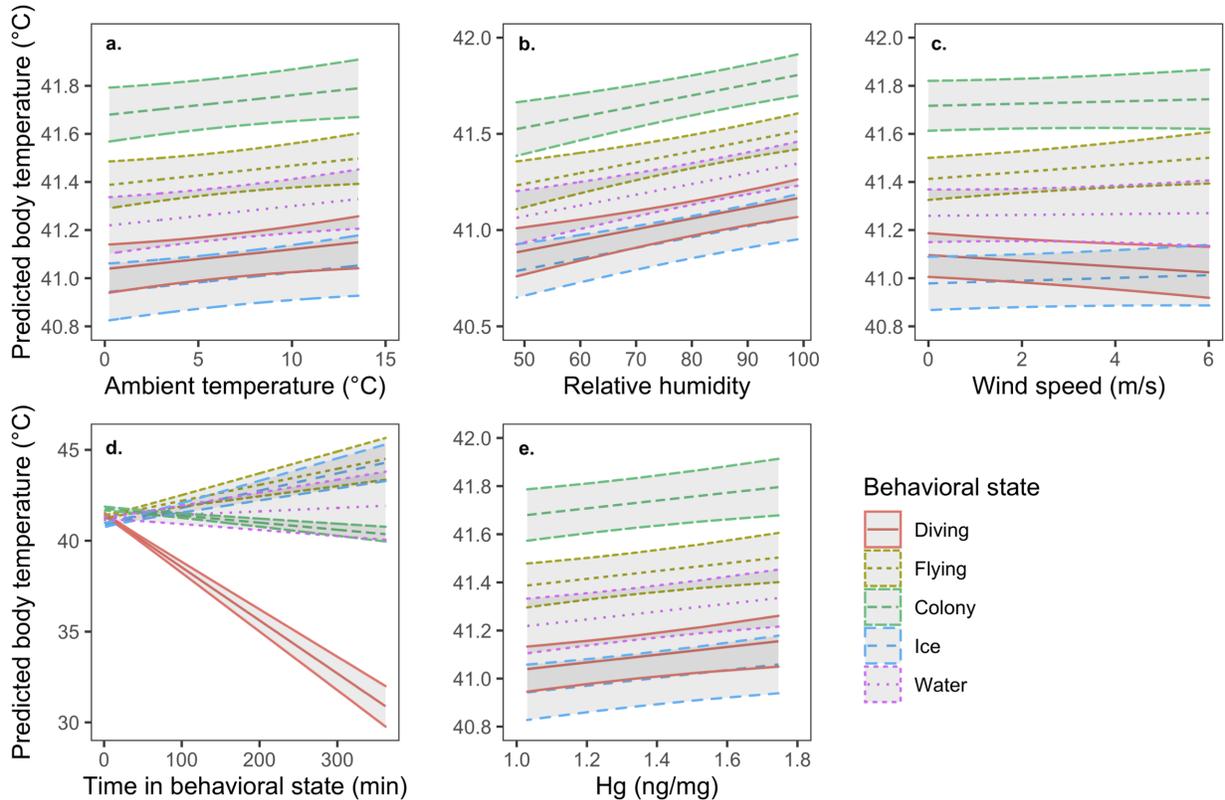
238 **Table 2.** Results of GAMMs predicting T_b within the behavioral states, showing estimated effects
 239 (Estimate \pm SE, t, P) of wind speed (m/s) (a), and time interval (min) within the behavioral bought (b).
 240 Differences in superscript letters indicate significant differences between trends.

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

241
 242 **Interaction with time in the behavioral state in predicting mean T_b and ΔT_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 ΔT_{bs} for the different behavioral states mostly aligned with the analysis above
 252 (Table S3). The ΔT_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 ΔT_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 ΔT_b for sea ice
 255 also greater than that of flying. The ΔT_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 (edf > 2) cyclic smooth spline term for the effect of time (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

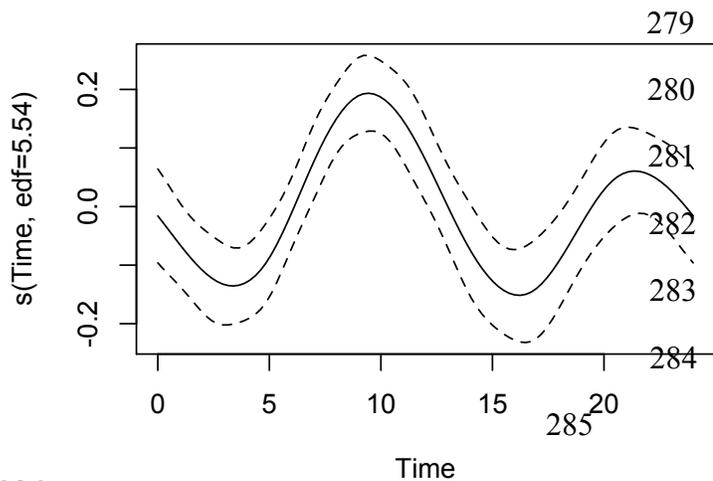


Figure 3. Residuals from the gamm model predicting mean T_b from time of day, with a smooth curve fitted. Dashed lines show 2-SE limits. The y-axis shows the partial effect of time on T_b .

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 ± 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 |

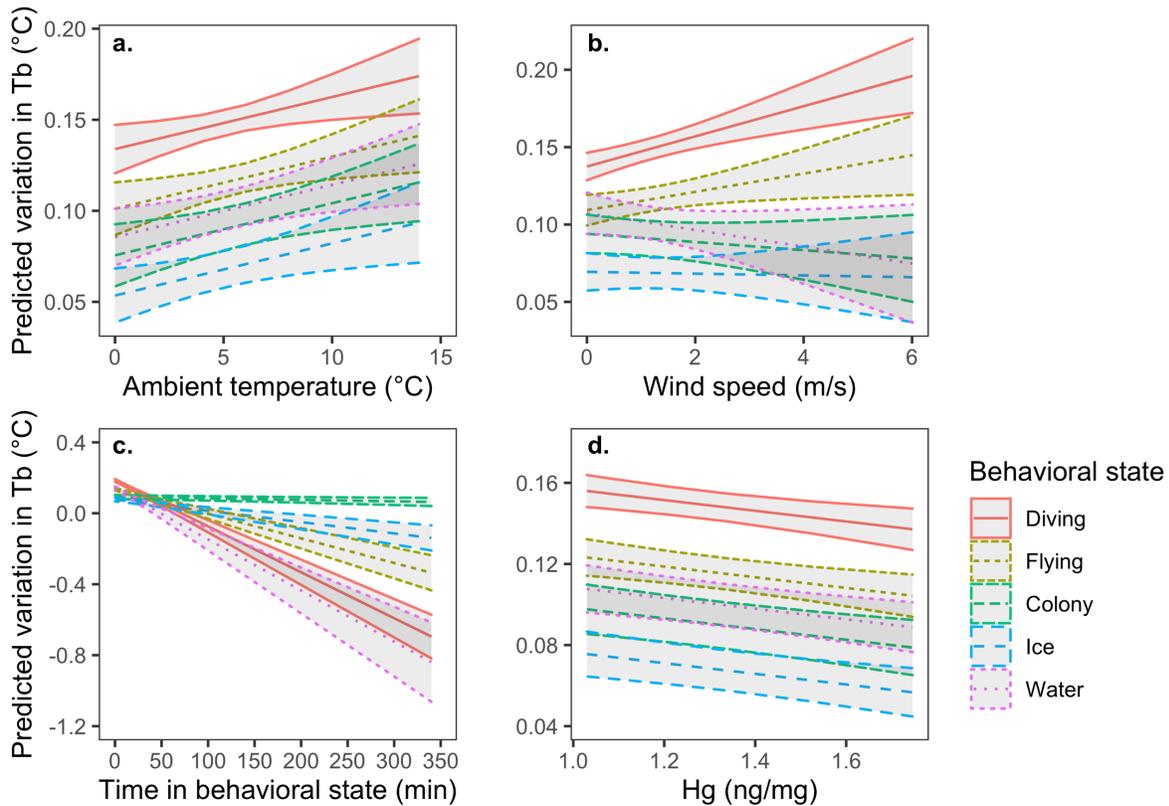
320

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 ^a | -0.003 \pm 0.0002, -10.99, <0.001 ^a |
| Colony | -0.003 \pm 0.002, -1.690, 0.091 ^b | -0.0001 \pm 0.0003, -2.586, 0.009 ^b |
| Ice | -0.001 \pm 0.002, -0.533, 0.594 ^b | -0.0006 \pm 0.0001, -9.966, <0.001 ^c |
| Flying | 0.007 \pm 0.003, 2.585, 0.010 ^{a,b} | -0.002 \pm 0.0002, -8.580, <0.001 ^d |
| Water | -0.006 \pm 0.004, -1.608, 0.108 ^b | -0.003 \pm 0.0004, -8.557, <0.001 ^a |

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 (β
337 \pm SE = -0.026 ± 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 ~ 7.24 x 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

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493
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495
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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
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