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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 rates¹, posing physiological and bioenergetic
47 challenges for organisms²⁻⁴. Among direct effects of shifting weather regimes on animals,
48 thermoregulatory challenges are particularly important⁵⁻⁹. Organisms are increasingly facing challenging
49 thermal environments in the form of elevated temperatures, extreme heat events and stochasticity¹. In
50 addition, other environmental conditions, such as wind patterns and humidity affect heat exchange with
51 the environment^{10,11}, and may evolve under climate change¹. 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 thermoregulation¹². Furthermore, in the Arctic, which is warming ~4 times faster than other regions^{1,13},
56 advanced melting and decreased extent of sea ice may mean longer commutes to favorable foraging
57 areas¹⁴ and loss of an important resting substrate that provides thermal relief at sea¹⁵.

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 mercury¹⁶, and global
61 warming has potential to exacerbate this threat¹⁷⁻¹⁹. 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^{16,20,21}. The methylated form, methylmercury
64 (MeHg) is especially bioavailable and harmful to wildlife²². Exposure of animals to MeHg may be
65 exacerbated by climate change²³. For instance, conversion of inorganic Hg to MeHg is potentiated in
66 warming oceans²⁴. Hg contamination may interfere with body temperature (T_b) regulation via endocrine
67 disruption²⁵, notably affecting production of thyroid hormones, which are central to thermoregulation²⁶. In
68 addition, Hg contamination could affect patterns of thermoregulation through effects on detoxification
69 costs and resting metabolic rate²⁷⁻²⁹. Although few data specific to Hg are available, both hypo- and
70 hyperthermic responses can occur in response to contamination³⁰. Hypothermic responses are proposed to
71 reflect an adaptive detoxification mechanism through which toxicity is reduced through facultative
72 reduction in T_b ^{30,31}. 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 flight³². 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^{33,34}. 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^{34,35}. 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 stability³⁵. 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 colonies³⁶. Both males and female incubate a single egg, and contribute
111 equally to provisioning of the chick^{37,38}. 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 chick³⁸. 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_b 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^{39,40} and body
117 condition¹⁴, 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_b 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_b 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^{41,42}. Birds spontaneously ingested T_b 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[®] 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^{37,38}. 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 colony⁴³).

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 in¹⁵). 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 diveMove⁴⁴, which applies the methods of
155 ⁴⁵ and ⁴⁶ 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 MeHg⁴⁷.
171 Samples were analyzed in duplicate using an Advanced Mercury Analyser spectrophotometer (Altec
172 AMA 254) at the Institute Littoral Environnement et Sociétés (LIENSs)⁴⁸. 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 3.6.1⁴⁹. We used generalized additive mixed effect models
180 (GAMMs) in R package mgcv^{50,51} 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 autocorrelation⁵², 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 models⁵³. We used package emmeans⁵⁴ 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 ΔT_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` package⁵⁵. 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 ± 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 ± 0.092 [41.4, 41.7]
215 $^\circ\text{C}$), at the colony (41.4 ± 0.089 [41.2, 41.6] $^\circ\text{C}$), on sea ice (41.4 ± 0.088 [41.2, 41.6] $^\circ\text{C}$), or on the water
216 (41.4 ± 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 ~ 19 minutes, from
220 ~ 41.5 to 40.6°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 ~ 90 min, from 41.9 to 40.9°C (Fig. 1a). On the other hand, T_b
222 increased the longer birds spent flying to ~ 15 minutes, from ~ 41.3 to 41.6°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 ~ 40.8 to 41.4°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 ΔT_b for diving was negative, with the 95% CI not overlapping zero (EMM \pm SE [95% CI]
227 = -0.312 ± 0.026 [-0.374, -0.251] $^\circ\text{C}$), and was lower than all other ΔT_b (Table S3 for pairwise
228 comparisons). The ΔT_b for flying and on sea ice were positive, with CIs not overlapping zero (EMM \pm SE
229 [95% CI] = 0.146 ± 0.029 [0.077, 0.215] $^\circ\text{C}$; 0.335 ± 0.045 [0.228, 0.443] $^\circ\text{C}$), and were higher than all
230 other ΔT_b , with ΔT_b for sea ice also greater than that of flying (Table S3 for pairwise comparisons). The

231 overall ΔT_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 ± 0.044 [-0.179,
 233 0.031] °C; 0.0002 ± 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>					
Variables	$\beta \pm SE$	<i>t</i>	<i>P</i>>(<i>t</i>)	<i>F</i>	<i>P</i>(><i>F</i>)
Intercept	40.6 \pm 0.464	87.414	< 0.001		
Flying ^a	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>					
	<i>edf</i>	<i>Ref.df</i>	<i>F</i>	<i>P</i>(><i>F</i>)	
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	
R-adjusted	0.212	N	16405, 8		

237 ^aRelative to diving

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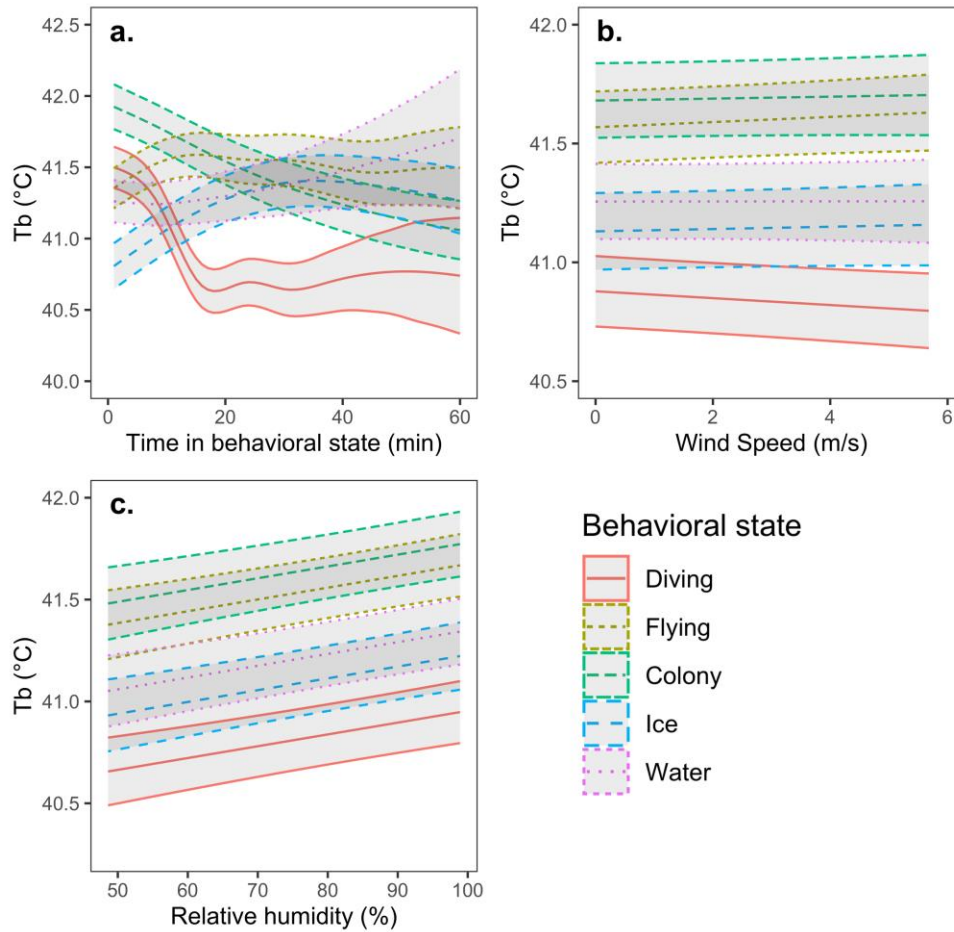
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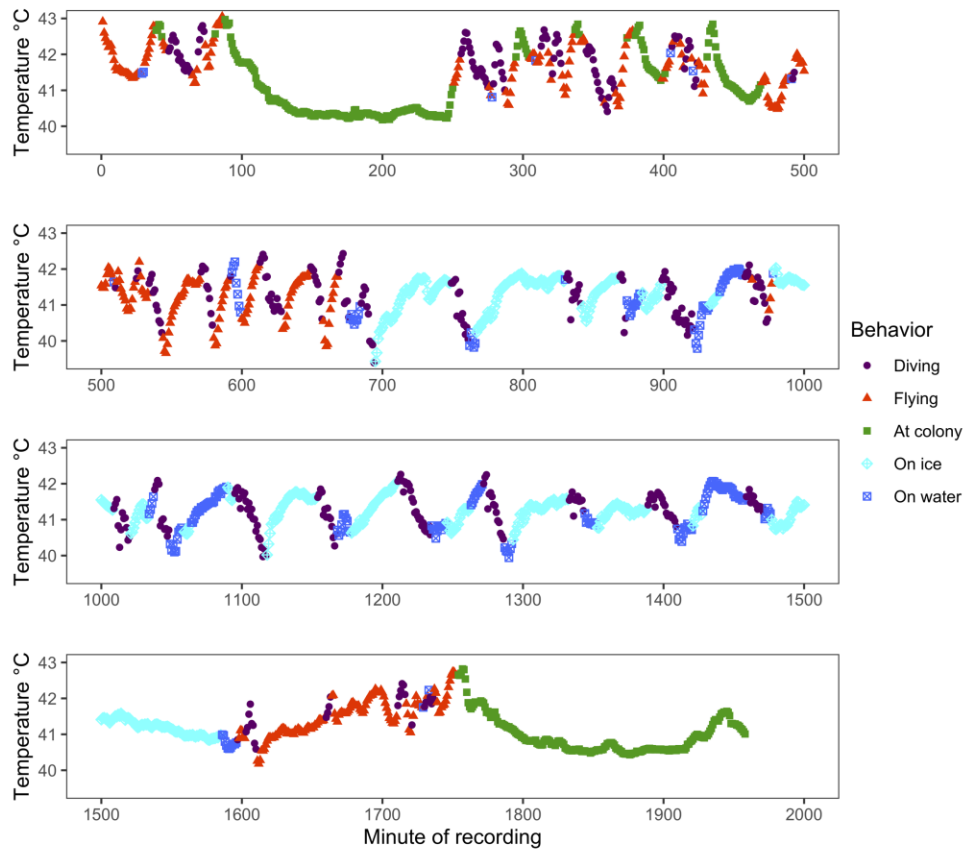
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245 **Figure 1.** Relationships between T_b (°C) of little auks predicted from the GAMM and (a) time within the
 246 behavioral state (min), (b) wind speed (m/s), and (c) Relative humidity (%). Shaded regions show 95%
 247 CIs.

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).

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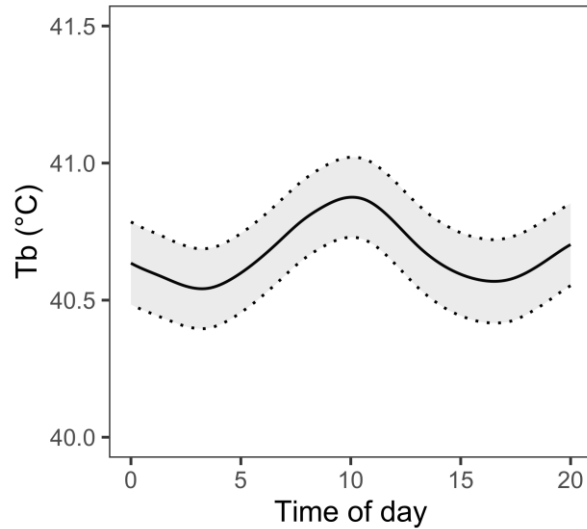
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Figure 2. Body temperature (T_b) through time color coded with respect to behavioral state for one little auk (LIAK20EG19) from the Ukaleqarteq, East Greenland, population. Note rebounds in T_b when on sea ice following declines while diving in cold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

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



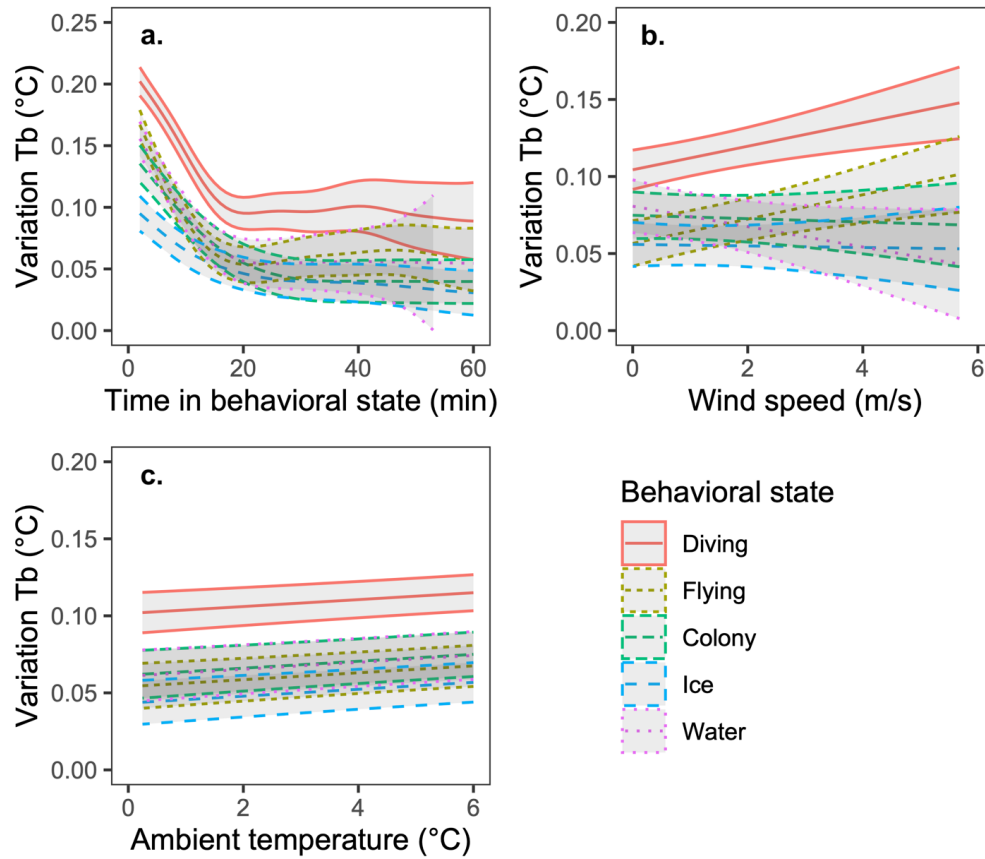
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269 **Figure 3.** Relationship between T_b ($^{\circ}\text{C}$) of little auks predicted from the GAMM and time of day. Shaded
 270 regions show 95% Cis.

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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 $^{\circ}\text{C}$), 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 ± 0.008 [0.080, 0.113] $^{\circ}\text{C}$), followed by flying (0.060 ± 0.008 [0.044, 0.077]
 276 $^{\circ}\text{C}$), on the water (0.055 ± 0.011 [0.033, 0.078] $^{\circ}\text{C}$), at the colony (0.041 ± 0.008 [0.024, 0.057] $^{\circ}\text{C}$) and
 277 on sea ice (0.040 ± 0.007 [0.025, 0.054] $^{\circ}\text{C}$), 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 ~ 15 min), and slightly more gradual at the colony (slope of $\sim -0.004^{\circ}\text{C min}^{-1}$ in
 283 the first ~ 25 min) and on the sea ice (slope of ~ -0.002 in the first ~ 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).

301
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>					
Variable	$\beta \pm \text{SE}$	<i>t</i> -value	<i>P</i> (> <i>t</i>)	<i>F</i>	<i>P</i> (> F)
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> (> F)	
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	
R²-adjusted	0.234	N	15136, 8		

304
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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312

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314

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

317

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^{14,56,57}, 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^{34,58,59}. 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 events⁶⁰, but our data lacked resolution to achieve this end. In another Alcid, Brünnich's
332 guillemots (*Uria lomvia*), T_b declined over sequential diving bouts³⁵. However, this decline occurred

333 during periods of resting on the water. During dives themselves, T_b increased and the peripheral
334 temperature declined³⁵. This pattern contrasts to T_b declines during diving observed in some penguin
335 species^{59,61,62}, and may reflect peripheral vasoconstriction and high wing beat frequency that generates
336 heat³⁵. 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 action⁶³), 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°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 coloration⁹. 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 species⁶⁵⁻⁶⁷.
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 dissipation⁶⁴.

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 activity³⁵. 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 ΔT_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^{33,68}. In
375 auks, compression of air space in feathers while diving reduces insulative properties, further facilitating
376 heat exchange with the environment⁶⁹. The costs of resting both in the air and on the water may be
377 reduced by warming temperatures⁷⁰. 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 species⁷¹. For example, in Brünnich's guillemot, the LCT in air and
381 water are 2 and 16°C , respectively^{71,72}, and the rate of increase in metabolic rate below the LCT is
382 substantially greater in water than in air (0.60 versus $0.17 \text{ W} \times \text{kg}^{-1} \text{ }^\circ\text{C}^{-1}$)⁷¹. 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 air⁷³. 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)¹⁵ 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 expenditure⁷⁴,
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 grounds⁷⁵. 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^{15,75}. Loss of sea ice as a substrate for resting, foraging, and movement has
398 demonstrated effects on energy balance in many sea ice-dependent species⁷⁶⁻⁷⁸. 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 declines⁷⁸.

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 ^{79,80}. 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 mode⁸¹, 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*)⁸². Hypothermic responses to contamination are hypothesized to reduce the toxicity of the
433 chemical in the body³⁰, 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 auks⁸³. 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.

458

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

465 **References**

- 466 ¹IPCC. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth
467 Assessment Report of the Intergovernmental Panel on Climate Change. Masson-Delmotte, V.,
468 Zhai, P., Pirani, A., Connors, S.L., Péan, C., *et al.* (eds.). Cambridge University Press (2021).
- 469 ²Humphries, M. M. Bioenergetic Prediction of Climate Change Impacts on Northern Mammals.
470 *Integrative and Comparative Biology*, **44**, 152–162. <https://doi.org/10.1093/icb/44.2.152> (2004).
- 471 ³Helmuth, B. From cells to coastlines: How can we use physiology to forecast the impacts of climate
472 change? *J. Exp. Biol.*, **212**, 753–760. <https://doi.org/10.1242/jeb.023861> (2009).
- 473 ⁴Dillon, M. E., Wang, G., & Huey, R. B. Global metabolic impacts of recent climate warming. *Nature*,
474 **467**, 704–706. <https://doi.org/10.1038/nature09407> (2010).
- 475 ⁵Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. Adaptive Thermoregulation in Endotherms
476 May Alter Responses to Climate Change. *Int. Comp. Biol.*, **51**, 676–690.
477 <https://doi.org/10.1093/icb/icr053> (2011).
- 478 ⁶Cook, T. R., Martin, R., Roberts, J., Häkkinen, H., Botha, P., *et al.* Parenting in a warming world:
479 Thermoregulatory responses to heat stress in an endangered seabird. *Conserv. Physiol.*, **8**, coz109.
480 <https://doi.org/10.1093/conphys/coz109> (2020).
- 481 ⁷Choy, E. S., O’Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, *et al.* Limited heat tolerance in a
482 cold-adapted seabird: Implications of a warming Arctic. *J. Exp. Biol.*, **224**, jeb242168.
483 <https://doi.org/10.1242/jeb.242168> (2021).

484 ⁸O'Connor, R. S., Le Pogam, A., Young, K. G., Robitaille, F., Choy, *et al.* (2021). Limited heat tolerance
485 in an Arctic passerine: Thermoregulatory implications for cold-specialized birds in a rapidly
486 warming world. *Ecol. Evol.*, **11**, 1609–1619. <https://doi.org/10.1002/ece3.7141> (2021).

487 ⁹O'Connor, R. S., Le Pogam, A., Young, K. G., Love, O. P., Cox, C. J., *et al.* Warming in the land of the
488 midnight sun: Breeding birds may suffer greater heat stress at high- versus low-Arctic sites. *Proc.*
489 *Roy. Soc. B*, **289**, 20220300. <https://doi.org/10.1098/rspb.2022.0300> (2022).

490 ¹⁰Wolf, B. O., & Walsberg, G. E. Thermal Effects of Radiation and Wind on a Small Bird and
491 Implications for Microsite Selection. *Ecology*, **77**, 2228–2236. <https://doi.org/10.2307/2265716>
492 (1996).

493 ¹¹Freeman, M. T., Czenze, Z. J., Schoeman, K., & McKechnie, A. E. Adaptive variation in the upper
494 limits of avian body temperature. *Proc. Natl. Acad. Sci.*, **119**, e2116645119.
495 <https://doi.org/10.1073/pnas.2116645119> (2022).

496 ¹²Kearney, M., Shine, R., & Porter, W. P. The potential for behavioral thermoregulation to buffer “cold-
497 blooded” animals against climate warming. *Proc. Natl. Acad. Sci.*, **106**, 3835–3840.
498 <https://doi.org/10.1073/pnas.0808913106> (2009).

499 ¹³Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., *et al.* The Arctic has
500 warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.*, **3**, 168.
501 <https://doi.org/10.1038/s43247-022-00498-3> (2022).

502 ¹⁴Amélineau, F., Grémillet, D., Harding, A. M. A., Walkusz, W., Choquet, R., *et al.* Arctic climate change
503 and pollution impact little auk foraging and fitness across a decade. *Sci. Rep.*, **9**, 1014.
504 <https://doi.org/10.1038/s41598-018-38042-z> (2019).

505 ¹⁵Grunst, A. S., Grunst, M. L., Grémillet, D., Kato, A., Bustamante, P., *et al.* Mercury Contamination
506 Challenges the Behavioral Response of a Keystone Species to Arctic Climate Change. *Environ.*
507 *Sci. Technol.*, **57**, 2054–2063. <https://doi.org/10.1021/acs.est.2c08893> (2023).

508 ¹⁶AMAP, 2021. AMAP Mercury Assessment. Summary for Policy-makers. Arctic Monitoring and
509 Assessment Programme (AMAP), Tromsø, Norway. 16 pp. (2021).

- 510 ¹⁷Jenssen, B. M. Endocrine-Disrupting Chemicals and Climate Change: A Worst-Case Combination for
511 Arctic Marine Mammals and Seabirds? *Environ. Health Persp.*, **114**, 76–80.
512 <https://doi.org/10.1289/ehp.8057> (2006).
- 513 ¹⁸Hooper, M. J., Ankley, G. T., Cristol, D. A., Maryoung, L. A., Noyes, P. D., *et al.* Interactions between
514 chemical and climate stressors: A role for mechanistic toxicology in assessing climate change
515 risks. *Environ. Toxicol. Chem.*, **32**, 32–48. <https://doi.org/10.1002/etc.2043> (2013).
- 516 ¹⁹Grunst, A. S., Grunst, M. L., & Fort, J. Contaminant-by-environment interactive effects on animal
517 behavior in the context of global change: Evidence from avian behavioral ecotoxicology. *Sci. Tot.*
518 *Environ.*, **879**, 163169. <https://doi.org/10.1016/j.scitotenv.2023.163169> (2023).
- 519 ²⁰Morel, F. M. M., Kraepiel, A. M. L., & Amyot, M. The chemical cycle and bioaccumulation of
520 mercury. *Ann. Rev. Ecol. System.*, **29**, 543–566. <https://doi.org/10.1146/annurev.ecolsys.29.1.543>
521 (1998).
- 522 ²¹Jonsson, S., Mastromonaco, M. N., Wang, F., Bravo, A. G., Cairns, W. R. L., *et al.* Arctic
523 methylmercury cycling. *Sci. Tot. Environ.*, **850**, 157445.
524 <https://doi.org/10.1016/j.scitotenv.2022.157445> (2022).
- 525 ²²Whitney, M. C., & Cristol, D. A. Impacts of Sublethal Mercury Exposure on Birds: A Detailed Review.
526 In P. de Voogt (ed.), *Rev. Environ. Contam. Toxicol.*, **244**, 113-163. Springer International
527 Publishing. https://doi.org/10.1007/398_2017_4 (2017).
- 528 ²³Mckinney, M. A., Pedro, S., Dietz, R., Sonne, C., Fisk, A. T., *et al.* A review of ecological impacts of
529 global climate change on persistent organic pollutant and mercury pathways and exposures in
530 arctic marine ecosystems. *Curr. Zool.*, **61**, 617–628. <https://doi.org/10.1093/czoolo/61.4.617>
531 (2015).
- 532 ²⁴Cossa, D. Methylmercury manufacture. *Nat. Geosci.*, **6**, 810–811. <https://doi.org/10.1038/ngeo1967>
533 (2013).

- 534 ²⁵Rice, K. M., Walker, E. M., Wu, M., Gillette, C., & Blough, E. R. Environmental Mercury and Its Toxic
535 Effects. *J. Prevent. Med. Pub.Health*, **47**, 74–83. <https://doi.org/10.3961/jpmph.2014.47.2.74>
536 (2014).
- 537 ²⁶Wada, H., Cristol, D. A., McNabb, F. M. A., & Hopkins, W. A. Suppressed adrenocortical responses
538 and thyroid hormone levels in birds near a mercury-contaminated river. *Environ. Sci. Technol.*,
539 **43**, 6031–6038. <https://doi.org/10.1021/es803707f> (2009).
- 540 ²⁷Calow, P. Physiological costs of combating chemical toxicants: Ecological implications. *Comp.*
541 *Biochem. Physiol. C*, **100**, 3–6. [https://doi.org/10.1016/0742-8413\(91\)90110-F](https://doi.org/10.1016/0742-8413(91)90110-F) (1991).
- 542 ²⁸Gerson, A. R., Cristol, D. A., & Seewagen, C. L. Environmentally relevant methylmercury exposure
543 reduces the metabolic scope of a model songbird. *Environ. Pollut.*, **246**, 790–796.
544 <https://doi.org/10.1016/j.envpol.2018.12.072> (2019).
- 545 ²⁹Seewagen, C. L., Elowe, C. R., Gerson, A. R., Groom, D. J. E., Ma, Y., *et al.* Short-term mercury
546 exposure disrupts muscular and hepatic lipid metabolism in a migrant songbird. *Sci. Rep.*, **12**,
547 11470. <https://doi.org/10.1038/s41598-022-15680-y> (2022).
- 548 ³⁰Leon, L. R. Thermoregulatory responses to environmental toxicants: The interaction of thermal stress
549 and toxicant exposure. *Toxicol. App. Pharmacol.*, **233**, 146–161.
550 <https://doi.org/10.1016/j.taap.2008.01.012> (2008).
- 551 ³¹Noyes, P. D., McElwee, M. K., Miller, H. D., Clark, B. W., Van Tiem, L. A., *et al.* The toxicology of
552 climate change: Environmental contaminants in a warming world. *Environ. Int.*, **35**, 971–986.
553 <https://doi.org/10.1016/j.envint.2009.02.006> (2009).
- 554 ³²Ste-Marie, E., Grémillet, D., Fort, J., Patterson, A., Brisson-Curadeau, É., *et al.* Accelerating animal
555 energetics: High dive costs in a small seabird disrupt the dynamic body acceleration–energy
556 expenditure relationship. *J. Exp. Biol.*, **225**, jeb243252. <https://doi.org/10.1242/jeb.243252>
557 (2022).
- 558 ³³Grémillet, D., Kuntz, G., Woakes, A. J., Gilbert, C., Robin, J.-P., *et al.* Year-round recordings of
559 behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving

560 endotherm during the Arctic winter. *J. Exp. Biol.*, **208**, 4231–4241.
561 <https://doi.org/10.1242/jeb.01884> (2005).

562 ³⁴Favilla, A. B., & Costa, D. P. Thermoregulatory Strategies of Diving Air-Breathing Marine Vertebrates:
563 A Review. *Front. Ecol. Evol.*, **8**, 555509. <https://doi.org/10.3389/fevo.2020.555509> (2020).

564 ³⁵Niizuma, Y., Gabrielsen, G. W., Sato, K., Watanuki, Y., & Naito, Y. Brünnich’s guillemots (*Uria*
565 *lomvia*) maintain high temperature in the body core during dives. *Comp. Biochem. Physiol. A*,
566 **147**, 438–444. <https://doi.org/10.1016/j.cbpa.2007.01.014> (2007).

567 ³⁶Egevang, C., Boertmann, D., Mosbech, A., & Tamstorf, M. P. Estimating colony area and population
568 size of little auks *Alle alle* at Northumberland Island using aerial images. *Polar Biol.*, **26**, 8–13.
569 <https://doi.org/10.1007/s00300-002-0448-x> (2003).

570 ³⁷Wojczulanis-Jakubas, K., Jakubas, D., & Stempniewicz, L. Sex-specific parental care by incubating
571 little auks (*Alle alle*). *Ornis Fenn.*, **86**, 140–148 (2009).

572 ³⁸Montevecchi, W. A. & Stenhouse, I. J. (2020). Dovekie (*Alle alle*), version 1.0. In *Birds of the World*
573 (Billerman, S. M., ed.) Cornell Lab of Ornithology, Ithaca, NY,
574 USA. <https://doi.org/10.2173/bow.doveki.01> (2020).

575 ³⁹Fort, J., Robertson, G. J., Grémillet, D., Traisnel, G., & Bustamante, P. Spatial Ecotoxicology:
576 Migratory Arctic Seabirds Are Exposed to Mercury Contamination While Overwintering in the
577 Northwest Atlantic. *Environ. Sci. Technol.*, **48**, 11560–11567. <https://doi.org/10.1021/es504045g>
578 (2014).

579 ⁴⁰Carravieri, A., Lorioux, S., Angelier, F., Chastel, O., Albert, C., *et al.* Carryover effects of winter
580 mercury contamination on summer concentrations and reproductive performance in little auks.
581 *Environ. Pollut.*, **318**, 120774. <https://doi.org/10.1016/j.envpol.2022.120774> (2023).

582 ⁴¹Tattersall, G. J., Roussel, D., Voituron, Y., & Teulier, L. Novel energy-saving strategies to multiple
583 stressors in birds: The ultradian regulation of body temperature. *Proc. Roy. Soc. B*, **283**,
584 20161551. <https://doi.org/10.1098/rspb.2016.1551> (2016).

585 ⁴²Gauchet, L., Jaeger, A., & Grémillet, D. Using facial infrared thermography to infer avian body
586 temperatures in the wild. *Mar. Biol.*, **169**, 57. <https://doi.org/10.1007/s00227-022-04041-y>
587 (2022).

588 ⁴³Amélineau, F., Grémillet, D., Bonnet, D., Le Bot, T., & Fort, J. Where to Forage in the Absence of Sea
589 Ice? Bathymetry As a Key Factor for an Arctic Seabird. *PLOS ONE*, **11**, e0157764.
590 <https://doi.org/10.1371/journal.pone.0157764> (2016).

591 ⁴⁴Luque, S.P. Diving Behaviour Analysis in R. *R News*, **7**, 8-14 (2007).

592 ⁴⁵Sibly, R. M., Nott, H. M. R., & Fletcher, D. J. Splitting behaviour into bouts. *Anim. Behav.*, **39**, 63–69.
593 [https://doi.org/10.1016/S0003-3472\(05\)80726-2](https://doi.org/10.1016/S0003-3472(05)80726-2) (1990).

594 ⁴⁶Mori, Y., Yoda, K., & Sato, K. Defining dive bouts using a sequential difference analysis. *Behaviour*,
595 **138**, 1451–1466. <https://doi.org/10.1163/156853901317367690> (2001).

596 ⁴⁷Chastel, O., Fort, J., Ackerman, J. T., Albert, C., Angelier, F., *et al.* Mercury contamination and
597 potential health risks to Arctic seabirds and shorebirds. *Sci. Tot. Environ.*, **844**, 156944.
598 <https://doi.org/10.1016/j.scitotenv.2022.156944> (2022).

599 ⁴⁸Bustamante, P., Lahaye, V., Durnez, C., Churlaud, C., & Caurant, F. Total and organic Hg
600 concentrations in cephalopods from the North Eastern Atlantic waters: Influence of geographical
601 origin and feeding ecology. *Sci.Tot. Environ.*, **368**, 585–596.
602 <https://doi.org/10.1016/j.scitotenv.2006.01.038> (2006).

603 ⁴⁹R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical
604 Computing, Vienna, Austria. <https://www.R-project.org/>. (2019).

605 ⁵⁰Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of
606 semiparametric generalized linear models: Estimation of Semiparametric Generalized Linear
607 Models. *J. Roy. Stat. Soc. B*, **73**, 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x> (2011).

608 ⁵¹Wood, S. N. *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman and
609 Hall/CRC. (2017).

610 ⁵²Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team. nlme: Linear and Nonlinear Mixed
611 Effects Models. R package version 3.1-143. <https://CRAN.R-project.org/package=nlme>. (2019).

612 ⁵³Schielzeth, H. Simple means to improve the interpretability of regression coefficients: *Interpretation of*
613 *regression coefficients. Meth. Ecol. Evo.*, **1**, 103–113. <https://doi.org/10.1111/j.2041->
614 [210X.2010.00012.x](https://doi.org/10.1111/j.2041-210X.2010.00012.x) (2010).

615 ⁵⁴Lenth, R. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.3.01.
616 <https://CRAN.R-project.org/package=emmeans> (2019).

617 ⁵⁵Lüdtke, D.ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J. Open Sour.*
618 *Soft.*, **3**, 772. <https://doi.org/10.21105/joss.00772> (2018).

619 ⁵⁶Kwasniewski, S., Gluchowska, M., Jakubas, D., Wojczulanis-Jakubas, K., Walkusz, W., *et al.* The
620 impact of different hydrographic conditions and zooplankton communities on provisioning Little
621 Auks along the West coast of Spitsbergen. *Prog. Oceanog.*, **87**, 72–82.
622 <https://doi.org/10.1016/j.pocean.2010.06.004> (2010).

623 ⁵⁷Grémillet, D., Welcker, J., Karnovsky, N., Walkusz, W., Hall, M., *et al.* Little auks buffer the impact of
624 current Arctic climate change. *Marine Ecology Progress Series*, **454**, 197–206.
625 <https://doi.org/10.3354/meps09590> (2012).

626 ⁵⁸Kooyman, G. L., & Ponganis, P. J. The physiological basis of diving depth: Birds and Mammals.
627 *Annual Review of Physiology*, **60**, 19–32. <https://doi.org/10.1146/annurev.physiol.60.1.19> (1998).

628 ⁵⁹Williams, C. L., & Ponganis, P. J. Diving physiology of marine mammals and birds: The development
629 of biologging techniques. *Philos. Trans. Roy. Soc. B*, **376**, 20200211.
630 <https://doi.org/10.1098/rstb.2020.0211> (2021).

631 ⁶⁰Wilson, R. P., Pütz, K., Grémillet, D., Culik, B. M., Kierspel, M., *et al.* Reliability of stomach
632 temperature changes in determining feeding characteristics of seabirds. *J. Exp. Biol.*, **198**, 1115–
633 1135. <https://doi.org/10.1242/jeb.198.5.1115> (1995).

- 634 ⁶¹Bevan, R. M., Butler, P. J., Woakes, A. J., & Boyd, I. L. The energetics of Gentoo Penguins, *Pygoscelis*
635 *papua*, during the breeding season: *Penguin energy expenditure. Funct. Ecol.*, **16**, 175–190.
636 <https://doi.org/10.1046/j.1365-2435.2002.00622.x> (2002).
- 637 ⁶²Green, J. A., Butler, P. J., Woakes, A. J., & Boyd, I. L. (2003). Energetics of diving in macaroni
638 penguins. *J. Exp. Biol.*, **206**, 43–57. <https://doi.org/10.1242/jeb.00059> (2003).
- 639 ⁶³Dawson, W. R., & O'Connor, T. P. Energetic Features of Avian Thermoregulatory Responses. In C.
640 Carey (ed.), *Avian Energetics and Nutritional Ecology*. 85–124. Springer US.
641 https://doi.org/10.1007/978-1-4613-0425-8_4 (1996).
- 642 ⁶⁴Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M., & Mehlum, F. Field and Laboratory Metabolism
643 and Thermoregulation in Dovekies (*Alle alle*). *The Auk*, **108**, 71-78
644 <http://doi.org.10.1093/auk/108.1.71> (1991).
- 645 ⁶⁵Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M., & Groothuis, T. G. G. Effect of social defeat in a
646 territorial bird (*Parus major*) selected for different coping styles. *Physiol. Behav.*, **73**, 427–433.
647 [https://doi.org/10.1016/S0031-9384\(01\)00492-9](https://doi.org/10.1016/S0031-9384(01)00492-9) (2001).
- 648 ⁶⁶Dezecache, G., Zuberbühler, K., Davila-Ross, M., & Dahl, C. D. Skin temperature changes in wild
649 chimpanzees upon hearing vocalizations of conspecifics. *Roy. Soc. Open*, **4**, 160816.
650 <https://doi.org/10.1098/rsos.160816> (2017).
- 651 ⁶⁷Knoch, S., Whiteside, M. A., Madden, J. R., Rose, P. E., & Fawcett, T. W. Hot-headed peckers:
652 Thermographic changes during aggression among juvenile pheasants (*Phasianus colchicus*).
653 *Philos. Trans. Roy. Soc. B*, **377**, 20200442. <https://doi.org/10.1098/rstb.2020.0442> (2022).
- 654 ⁶⁸Enstipp, M. R., Grémillet, D., & Lorentsen, S.-H. Energetic costs of diving and thermal status in
655 European shags (*Phalacrocorax aristotelis*). *J. Exp. Biol.*, **208**, 3451–3461.
656 <https://doi.org/10.1242/jeb.01791> (2005).
- 657 ⁶⁹Oswald, S. A., & Arnold, J. M. Direct impacts of climatic warming on heat stress in endothermic
658 species: Seabirds as bioindicators of changing thermoregulatory constraints. *Int. Zool.*, **7**, 121–
659 136. <https://doi.org/10.1111/j.1749-4877.2012.00287.x> (2012).

660 ⁷⁰Tremblay, F., Whelan, S., Choy, E. S., Hatch, S. A., & Elliott, K. H. Resting costs too: The relative
661 importance of active and resting energy expenditure in a sub-arctic seabird. *J. Exp. Biol.*, **225**,
662 jeb243548. <https://doi.org/10.1242/jeb.243548> (2022).

663 ⁷¹Croll, D. A., & McLaren, E. Diving metabolism and thermoregulation in common and thick-billed
664 murre. *J. Comp. Physiol. B*, **163**. <https://doi.org/10.1007/BF00263602> (1993).

665 ⁷²Gabrielsen, G. W., Mehlum, F., & Karlsen, H. E. Thermoregulation in four species of arctic seabirds. *J.*
666 *Comp. Physiol. B*, **157**, 703–708. <https://doi.org/10.1007/BF00691000> (1988).

667 ⁷³Richman, S. E., & Lovvorn, J. R. Effects of Air and Water Temperatures on Resting Metabolism of
668 Auklets and Other Diving Birds. *Physiol. Biochem. Zool.*, **84**, 316–332.
669 <https://doi.org/10.1086/660008> (2011).

670 ⁷⁴Lovvorn, J. R., Grebmeier, J. M., Cooper, L. W., Bump, J. K., & Richman, S. E. Modeling marine
671 protected areas for threatened eiders in a climatically changing Bering Sea. *Ecol. Appl.*, **19**, 1596–
672 1613. <https://doi.org/10.1890/08-1193.1> (2009).

673 ⁷⁵Grunst, M. L., Grunst, A. S., Grémillet, D., Kato, A., Bustamante, P., *et al.* A keystone avian predator
674 faces elevated energy expenditure in a warming Arctic. *Ecology*, **e4034**,
675 <https://doi.org/10.1002/ecy.4034> (2023).

676 ⁷⁶Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., *et al.* Ecological Consequences of Sea-Ice
677 Decline. *Science*, **341**, 519–524. <https://doi.org/10.1126/science.1235225> (2013).

678 ⁷⁷Laidre, K. L., Atkinson, S., Regehr, E. V., Stern, H. L., Born, E. W., *et al.* Interrelated ecological
679 impacts of climate change on an apex predator. *Ecol. Appl.*, **30**. <https://doi.org/10.1002/eap.2071>
680 (2020).

681 ⁷⁸Pagano, A. M., & Williams, T. M. Physiological consequences of Arctic sea ice loss on large marine
682 carnivores: Unique responses by polar bears and narwhals. *J. Exp. Biol.*, **224**, jeb228049.
683 <https://doi.org/10.1242/jeb.228049> (2021).

684 ⁷⁹Dawson, W. R. (1982). Evaporative losses of water by birds. *Comp. Biochem. Physiol. A*, **71**, 495–509.
685 [https://doi.org/10.1016/0300-9629\(82\)90198-0](https://doi.org/10.1016/0300-9629(82)90198-0) (1982).

686 ⁸⁰Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. The Impact of Humidity on
687 Evaporative Cooling in Small Desert Birds Exposed to High Air Temperatures. *Physiol. Biochem.*
688 *Zool.*, **87**, 782–795. <https://doi.org/10.1086/678956> (2014).

689 ⁸¹Elliott, K. H., Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A, *et al.* Windscaapes shape seabird
690 instantaneous energy costs but adult behavior buffers impact on offspring. *Mov. Ecol.*, **2**, 17.
691 <https://doi.org/10.1186/s40462-014-0017-2> (2014).

692 ⁸²Gordon, C. J., Fogelson, L., & Highfill, J. W. Hypothermia and hypometabolism: Sensitive indices of
693 whole-body toxicity following exposure to metallic salts in the mouse. *J. Toxicol. Environ.*
694 *Health*, **29**, 185–200. <https://doi.org/10.1080/15287399009531382> (1990).

695 ⁸³Wojczulanis-Jakubas, K., Wąż, P., & Jakubas, D. Little auks under the midnight sun: Diel activity
696 rhythm of a small diving seabird during the Arctic summer. *Pol. Res.*, **39**, 3309.
697 <https://doi.org/10.33265/polar.v39.3309> (2020).

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