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

2   **predator**

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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

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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

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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; ±1°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; $[Hg] = 0.292 \pm 0.022$ µg 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 µg g^{-1} dw and 0.306 ± 0.004 µg 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 bought

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   (deltas) 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_{bs} 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 (Lüdecke 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

8

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

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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).

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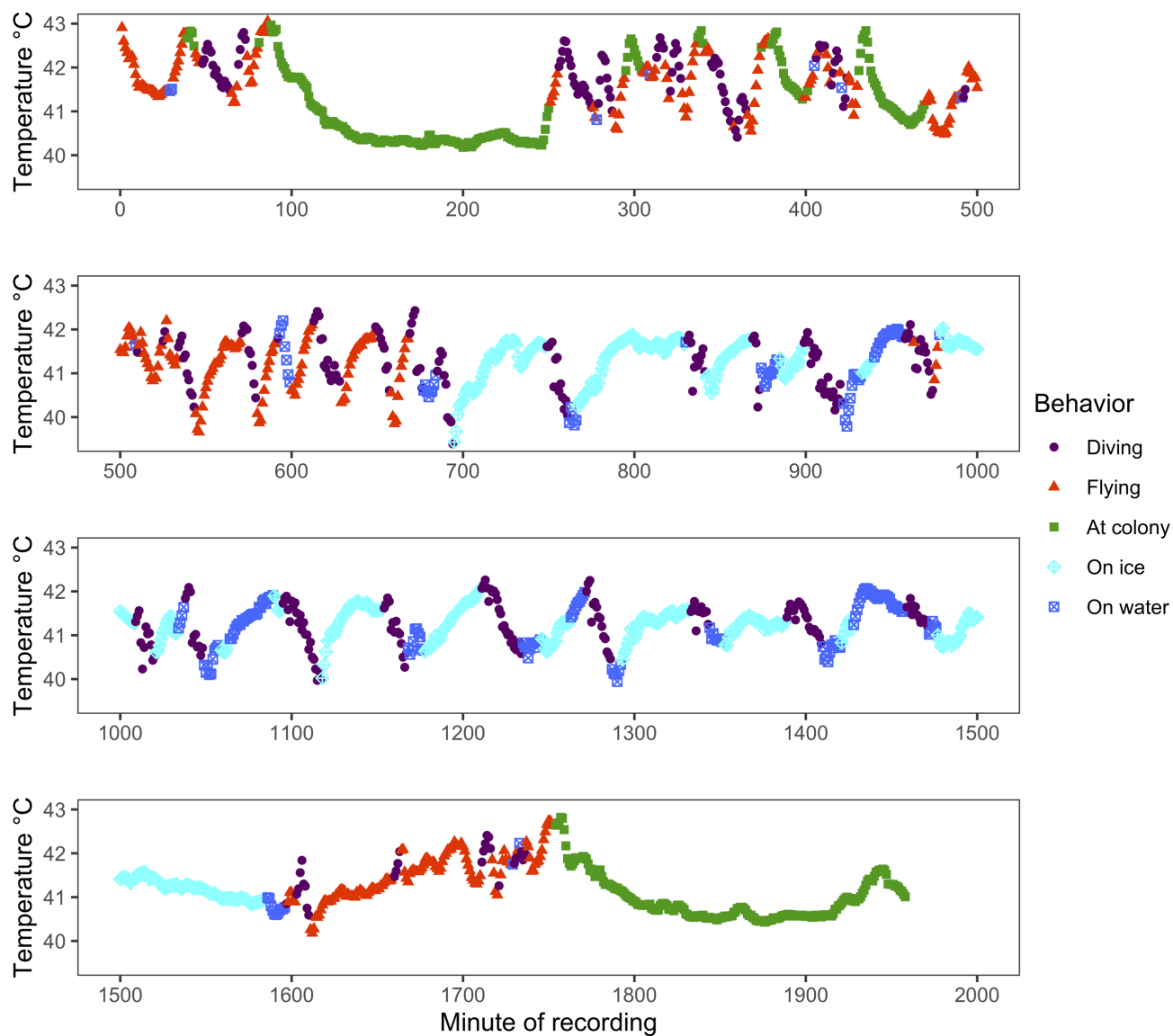
Figure 1. Variation in body temperature (T_b) through time and color coded with respect to behavioral state for one individual little auk (LIAK20EG19) from the Ukaleqarteq, East Greenland, population. Note rebounds in T_b when on the sea ice following declines while diving in cold arctic waters. T_b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

238   **Table 2.** Results of GAMMs predicting T_b within the behavioral states, showing estimated effects

239   (Estimate ± 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 ± 0.008, -0.853, 0.393^a	-0.024 ± 0.001, -15.15, $<0.001^a$
Colony	0.001 ± 0.005, 0.110, $0.913^{a,c}$	-0.004 ± 0.001, -5.807, $<0.001^b$
Ice	0.004 ± 0.004, 1.193, $0.233^{a,c}$	0.014 ± 0.001, 12.36, $<0.001^c$
Flying	0.015 ± 0.007, 2.265, $0.0236^{a,c}$	0.001 ± 0.0001, 1.580, 0.114^c
Water	0.001 ± 0.009, 0.148, $0.882^{b,c}$	0.001 ± 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),

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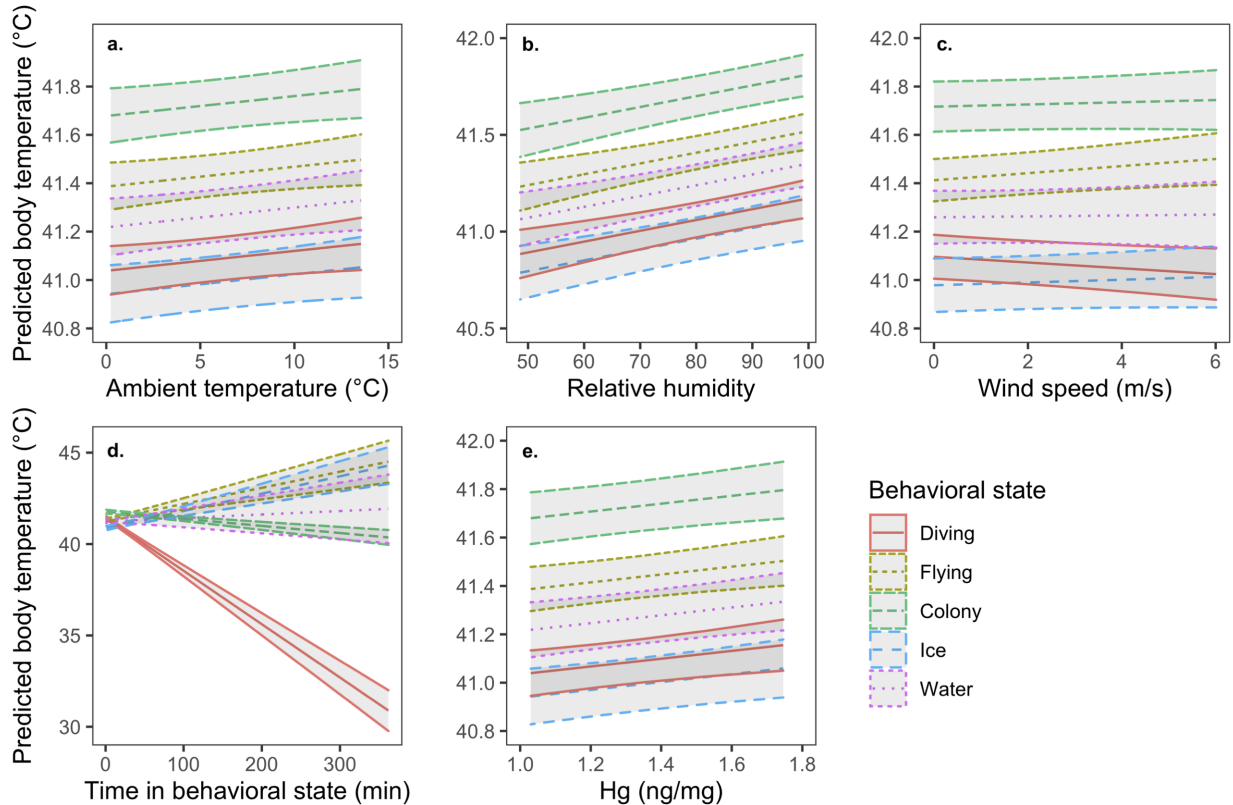
259

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 ± SE Hg concentration in the blood was $1.290 ± 0.031$ µg g^{-1}

266   dw [range: 1.030-1.746 µg g^{-1} dw], which assuming 79% blood moisture content is equivalent to $0.271 ±$

267   0.007 µg g^{-1} ww [range: 0.216-0.367 µg g^{-1} ww], and falls within the range of low risk for toxicological

268   effects (0.2–1.0 µg 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 (β ± SE = $0.161 ± 0.061$, $t =$

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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

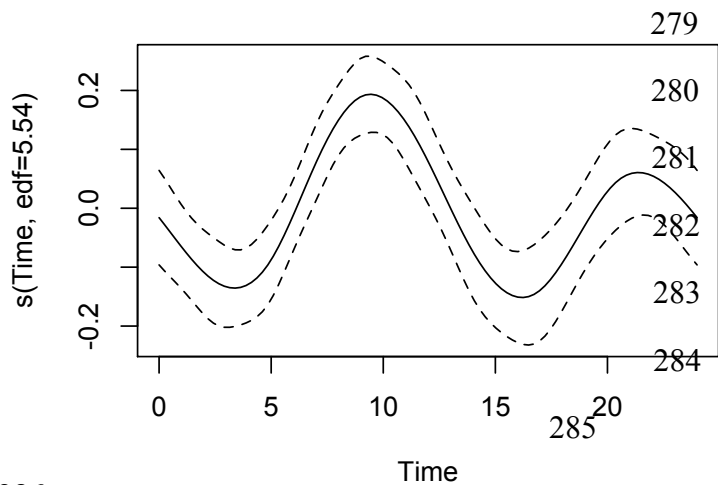277   the lowest values in the early morning (~4:00 am) (Fig. 3).

278

279   **Figure 3**. Residuals from the gamm model

280   predicting mean T_b from time of day, with a

281   smooth curve fitted. Dashed lines show 2-SE

282   limits. The y-axis shows the partial effect of time

283   on T_b.

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287   **Effect of behavioral state on between minute variation in T_b**: The mean ± 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

14

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

320

16

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 ± 0.003, 3.054, 0.002^a	-0.003 ± 0.0002, -10.99, $<0.001^a$
Colony	-0.003 ± 0.002, -1.690, 0.091^b	-0.0001 ± 0.0003, -2.586, 0.009^b
Ice	-0.001 ± 0.002, -0.533, 0.594^b	-0.0006 ± 0.0001, -9.966, $<0.001^c$
Flying	0.007 ± 0.003, 2.585, $0.010^{a,b}$	-0.002 ± 0.0002, -8.580, $<0.001^d$
Water	-0.006 ± 0.004, -1.608, 0.108^b	-0.003 ± 0.0004, -8.557, $<0.001^a$

324

325
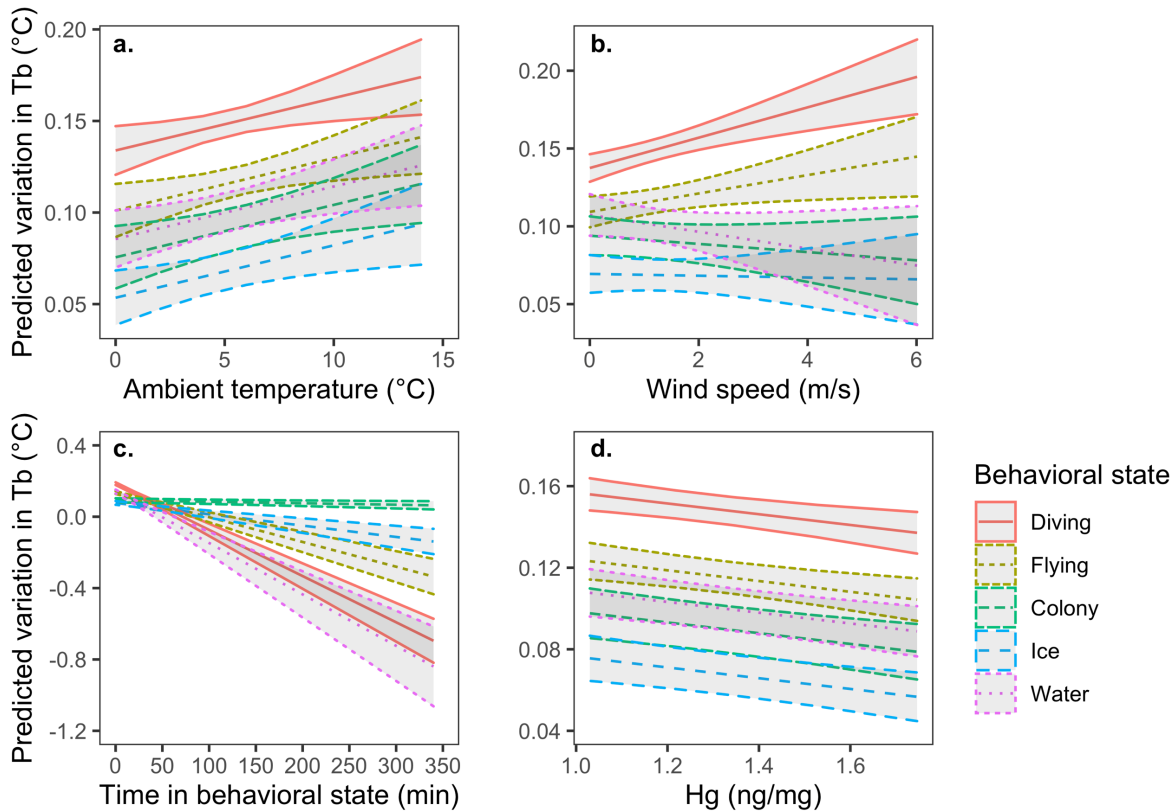
326

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 $= -0.026 \pm 0.008$, $t = -3.193$, $P = 0.001$; Fig. 4d).

338

339   **Effect of time of day on between minute variation in T_b**: Between minute variation in T_b did not vary

340   with time of day (edf $= 0.949$, $F_8 = 0.226$, $P = 0.127$).

341

342   **Discussion**

343   Although T_b in little auks was relatively tightly regulated around a mean of 41.02 °C, we observed low,

344   but significant, variation according to behavioral state and weather conditions. Such plasticity may be

345   critical to maintaining energy balance across contexts and may buffer species against negative fitness

346   effects in the context of global change. Nevertheless, the potential for plasticity to prevent energetic costs

347   is not infinite, and our study suggested potential thermoregulatory challenges under global climate change

348   scenarios. In particular, T_b rebounded on sea ice following declines during diving episodes in frigid Artic

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

18

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 ~0.33°C, meaning that, on average, they approximately recovered the amount of T_b lost while

362   foraging, that is, ~0.31°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 (~25 ×) 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

20

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 our 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

21

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

22

456   Ponganis 2021), and was interpreted as reflecting a combination of peripheral vasoconstriction and high

457   wing beat frequency that generates heat (Niizuma et al. 2007). Our data lack the resolution to effectively

458   separate dives from inter-dive intervals. Thus, a similar dynamic could also be occurring in our birds.

459   Finally, the best model predicting mean T_b included a non-linear effect of time, with the highest values

460   occurring around mid-day and the lowest values in the early morning. Despite the fact that little auks in

461   our population breed under 24-hrs of daylight, this diurnal variation in T_b may reflect timing of maximum

462   solar radiation exposure, a diel pattern of activity levels, and/or underlying circadian rhythmicity in T_b

463   independent of activity levels. A past study on little auks found a regular rhythm of population attendance

464   at the population level, likely associated with period of lower predation pressure, which provides some

465   foundation for expecting that T_b could also display a diel pattern of variation. However, this same study

466   found little circadian rhythm in activity patterns of individual little auks (Wojczulanis-Jakubas et al.

467   2020), In contrast to mean T_b, between minute variation in T_b did not show a pattern with time of day.

468

469   **Conclusions**: Our results demonstrate that the T_b of little auks is modulated according to both behavioral

470   state and environmental conditions, which likely aids animals in maximizing energy balance while

471   performing essential behaviors in dynamic environments. Although this plasticity is predicted to facilitate

472   energy balance in the face of climate change, the dynamic nature of T_b regulation also suggests that

473   changing environmental conditions may significantly alter energy balance, or the behavioral and energetic

474   strategies that must be adopted to achieve energetic homeostasis. Most notably, our data suggests that

475   little auks use sea ice as a thermal refuge, resting on this substrate to allow T_b to rebound after submersion

476   in cold water. If sea ice is lost due to warming temperature, thermoregulatory costs are forecast to

477   increase substantially as birds are forced to instead rest on the water surface. Furthermore, the elevated

478   and less variable T_b of little auks with high Hg concentrations is of potential concern. Higher T_b in

479   contaminated birds could elevate energetic costs or limit plasticity, further challenging scope for

480   maintaining energy balance under scenarios of environmental change.

481

482   **Data availability**: Data will be made available via the Zenodo community of European Commission

483   Funded Research (OpenAIRE) (doi: 10.5281/zenodo.7220883).

484

493

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

495

496   **Authors' contributions**: MLG, ASG and JF conceived the study. MLG, ASG, DG and JF obtained

497   funding for fieldwork and laboratory analyses. MSG, ALG, SG and JF collected the data. MLG, ASG and

498   AS analysed the data. MLG and ASG wrote the first draft of the manuscript. All authors read and

499   commented on the manuscript.

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501   **References**

502   Ackerman JT, Eagles-Smith CA, Herzog MP, Hartman CA, Peterson SH, Evers DC, et al. 2016. Avian

503   mercury exposure and toxicological risk across western North America: a synthesis. Sci Total

504   Environ. 568: 749-769.

505   Albert C, Renedo M, Bustamante P, Fort J. 2019. Using blood and feathers to investigate large-scale Hg

506   contamination in Arctic seabirds: a review. Environ Res. 177: 108588. doi:

507   10.1016/j.envres.2019.108588.

24

508   AMAP, 2021. 2021. AMAP Mercury Assessment. Summary for Policy-makers. Arctic Monitoring and

509   Assessment Programme (AMAP), Tromsø, Norway. 16 pp.

510   Amélineau F, Grémillet D, Harding AMA, Walkusz W, Choquet R, Fort J. 2018. Arctic climate change

511   and pollution impact little auk foraging and fitness across a decade. Sci Rep. 9: 1014. doi:

512   10.1038/s41598-018-38042-z.

513   Angilletta MJ, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal physiology in

514   endotherms. Front Biosci E2: 861–881. ddoi: 10.2741/e148.

515   Aulie A. 1971. Body temperatures in pigeons and budgerigars during sustained flight. Comp Biochem

516   Physiol A. 39: 173-176. doi: 10.1016/0300-9629(71)90074-0.

517   Bevan RM, Butler PJ, Woakes AJ, Boyd IL. 2002. The energetics of gentoo penguins, Pygoscelis papua,

518   during the breeding season. Funct Ecol. 16: 175–190. doi:10.1046/j.1365-2435.2002.00622.x.

519   Blévin P, Tartu S, Ellis HI, Chastel O, Bustamante P, Parenteau C, Herzke D, Angelier F, Gabrielsen

520   GW. 2017. Contaminants and energy expenditure in an Arctic seabird: Organochlorine pesticides

521   and perfluoroalkyl substances are associated with metabolic rate in a contrasted manner. Environ

522   Res. 157: 118–126. doi: 10.1016/j.envres.2017.05.022.

523   Brodin A, Nilsson JÅ, Nord A. 2017. Adaptive temperature regulation in the little bird in winter:

524   predictions from a stochastic dynamic programming model. Oecologia 185: 43-54. doi:

525   10.1007/s00442-017-3923-3.

526   Bruinzeel LW, Piersma T. 2008. Cost reduction in the cold: heat generated by terrestrial locomotion

527   partly substitutes for thermoregulatory costs in Knot Calidris canutus. Ibis 140: 323-328. doi:

528   10.1111/j.1474-919X.1998.tb04396.x.

529   Bustamante P, Lahaye V, Durnez C, Churlaud C, Caurant, F. 2006. Total and organic Hg concentrations in

530   cephalopods from the North Eastern Atlantic waters: Influence of geographical origin and feeding

531   ecology. Sci Total Environ. 368: 585–596. doi: 10.1016/j.scitotenv.2006.01.038.

532   Calow P. 1991. Physiological costs of combating chemical toxicants - ecological implications. Comp

533   Biochem Physiol C Comp Pharmacol Toxicol. 100: 3-6. doi: 10.1016/0742-8413(91)90110-f.

25

534 Careau V, Garland Jr. T. 2012. Performance, personality, and energetics: Correlation, causation, and

535   mechanism. Physiol Biochem Zool. 85: 543– 571. doi: 10.1086/666970.

536 Chastel O, Fort J, Ackerman JT, Albert C, Angelier F, Basu N, *et al*. 2022. Mercury contamination and

537   potential health risks to Arctic seabirds and shorebirds. Sci Total Environ. 844: 156944. doi:

538   10.1016/j.scitotenv.2022.156944.

539 Cooper CE, Hurley LL, Deviche P, Griffith SC. 2020. Physiological responses of wild zebra finch

540   (*Taeniopygia guttata*) to heatwaves. J Exp Biol. 223: jeb225524. doi: 10.1242/jeb.225524.

541 Crompton AW, Taylor CR, Jagger JA. 1978. Evolution of homeothermy in mammals. Nature 272: 333-

542   336. doi:10.1038/272333a0.

543 Dawson WR. 1982. Evaporative losses of water by birds. Comp Biochem Physiol A 71: 495-509. doi:

544   10.1016/0300-9629(82)90198-0.

545 Douglas TK, Cooper CE, Withers PC. 2017. Avian torpor or alternative thermoregulatory strategies for

546   overwintering? J Exp Biol. 220: 1341-1349. doi:10.1242/jeb.154633.

547 Enstipp MR, Grémillet D, Lorentsen S-H. 2005. Energetic costs of diving and thermal status in European

548   shags (*Phalacrocorax aristotelis*). J Exp Biol. 208:3451-3461. doi:10.1242/jeb.01791.

549 Favilla AB, Costa DP. 2020. Thermoregulatory Strategies of Diving Air-Breathing Marine Vertebrates: A

550   Review. Front Ecol Evol. 8: 555509. doi: 10.3389/fevo.2020.555509.

551 Fort J, Porter WP, Grémillet D. 2009. Thermodynamic modelling predicts energetic bottleneck for

552   seabirds wintering in the northwest Atlantic. J Exp Biol. 212: 2483–2490. doi:

553   10.1242/jeb.032300.

554 Fort J, Robertson GJ, Grémillet D, Traisnel G, Bustamante P. 2014. Spatial ecotoxicology: migratory

555   seabirds are exposed to mercury contamination while overwintering in the Northwest Atlantic.

556   Environ Sci Technol. 48: 11560-11567. doi: 10.1021/es504045g.

557 Gerson AR, Smith EK, Smit B, McKechnie AE, Wolf B. 2014. The impact of humidity on evaporative

558   cooling in small desert birds exposed to high air temperature. Physiol Biochem Zool. 87: 782-

559   795. doi: 10.1086/678956.

560 Gerson AR, McKechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, et al. 2019a. The functional

561 significance of facultative hyperthermia varies with body size and phylogeny in birds. Funct Ecol.

562 33: 597–607. doi: 10.1111/1365-2435.13274

563 Gerson AR, Cristol DA, Seewagen CL. 2019b. Environmentally relevant methylmercury exposure

564 reduces the metabolic scope of a model songbird. Environ Pollut. 246: 790–796. doi:

565 10.1016/j.envpol.2018.12.072.

566 Gordon CJ, Fogelson L, Highfill JW. 1990. Hypothermia and hypometabolism: Sensitive indices of

567 whole-body toxicity following exposure to metallic salts in the mouse. J Toxicol Environ Health

568 29: 185–200. doi: 10.1080/15287399009531382.

569 Green J, Butler P, Woakes A, Boyd I. 2003. Energetics of diving in macaroni penguins. J Exp Biol. 206:

570 43–57. doi:10.1242/jeb.00059.

571 Grémillet D, Kuntz G, Woakes AJ, Gilbert C, Robin J-P, Le Maho, Y, Butler PJ. 2005. Year-round

572 recordings of behavioural and physiological parameters reveal the survival strategy of a poorly

573 insulated diving endotherm during the Arctic winter. J Exp Biol. 208: 4231–4241. doi:

574 10.1242/jeb.01884.

575 Humphries MM, Careau V. 2011. Heat for nothing or activity for free? Evidence and implications for

576 activity-thermoregulatory heat substitution. Integ Comp Biol. 51:419-431. doi:

577 10.1093/icb/icr059.

578 Jenssen BM. 2006. Endocrine-disrupting chemicals and climate change: a worst-case combination for arctic

579 marine mammals and seabirds? Environ Health Persp. 114: 76. doi: 10.1289/ehp.8057.

580 Jonsson S, Mastromonaco MN, Wang F, Bravo AG, Cairns WRL, Chételat J, *et al.* 2022. Arctic

581 methylmercury cycling. Sci Total Environ. 850: 157445. doi: 10.1016/j.scitotenv.2022.157445.

582 Khaliq I, Hof C, Prinzinger R, Böhning-Gaese K, Pfenninger M. 2014. Global variation in thermal

583 tolerances and vulnerability of endotherms to climate change. Proc Roy Soc London B. 281:

584 20141097. doi: 10.1098/rspb.2014.1097.

585   Kooyman GL, Ponganis PJ. 1998. The physiological basis of diving at depth: birds and mammals.

586   Ann Rev Physiol. 60: 19–32. doi: 10.1146/annurev.physiol.60.1.19.

587   Laidre KL, Atkinson S, Regehr EV, Stern HL, Born EW, Wiig Ø, *et al*. 2020. Interrelated ecological

588   impacts of climate change on an apex predator. Ecol Appl. 30: e02071. doi: 10.1002/eap.2071.

589   Lenth R. 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version

590   1.4.3.01. https://CRAN.R-project.org/package=emmeans.

591   Leon LR. 2008. Thermoregulatory responses to environmental toxicants: The interaction of thermal stress

592   and toxicant exposure. Toxicol Appl Pharmacol. 233: 146–161. doi: 10.1016/j.taap.2008.01.012.

593   Lovvorn JR, Grebmeier JM, Cooper LW, Bump JK, Richman SE. 2009. Modeling marine protected areas

594   for threatened eiders in a climatically changing Bering Sea. Ecol Appl. 19: 1596–1613. doi:

595   10.1890/08-1193.1.

596   Lüdecke D. 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. J Open Sour

597   Software 3: 772. doi: 10.21105/joss.00772 (URL: https://doi.org/10.21105/joss.00772).

598   Luque, S.P. Diving Behaviour Analysis in R. R News 7: 8-14.

599   McKechnie AE, Lovegrove BG. 2002. Avian facultative hypothermic responses: a review. The Condor

600   104: 705-724. doi:10.1093/condor/104.4.705.

601   McKechnie AE, Wolf BO. 2019. The physiology of heat tolerance in small endotherms. Physiol. 34: 302-

602   313. doi: 10.1152/physiol.00011.2019.

603   Morel FMM, Kraepiel AML, Amyot M. 1998. The chemical cycle and bioaccumulation

604   of mercury. Annu Rev Ecol Syst. 29: 543–566. doi: 10.1146/annurev.ecolsys.29.1.543.

605   Mori Y, Yoda K, Sato K. 2001. Defining dive bouts using a sequential differences analysis. Behavior

606   138: 1451-1466. doi: 10.1163/156853901317367690.

607   Niizuma Y, Gabrielsen GW, Sato K, Watanuki Y, Naito Y. 2007. Brünnich's guillemots (Uria lomvia)

608   maintain high temperature in the body core during dives. Comp Biochem Physiol Part A: Mol Int

609   Physiol. 147: 438–444. doi: 10.1016/j.cbpa.2007.01.014.

610   Nilsson JÅ, Molokwu MN, Olsson O. 2016. Body temperature regulation in hot environments. PLoS One

611   11:e0161481. doi: 10.1371/journal.pone.0161481.

612   Noyes PD, McElwee MK, Miller HD, Clark BW, Van Tiem LAV, Walcott KC, Erwin KN, Levin ED.

613   2009. The toxicology of climate change: environmental contaminants in a warming world.

614   Environ Intern. 35: 971-986. doi: 10.1016/j.envint.2009.02.006.

615   Pagano AM, Williams TM. 2021. Physiological consequences of Arctic sea ice loss on large marine

616   carnivores: Unique responses by polar bears and narwhals. J Exp Biol. 224(Suppl_1): jeb228049.

617   doi: 10.1242/jeb.228049.

618   Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2019. nlme: Linear and Nonlinear Mixed Effects

619   Models. R package version 3.1-143, <URL: https://CRAN.R-project.org/package=nlme>.

620   Ponganis PJ, Van Dam RP, Levenson DH, Knower T, Ponganis KV, Marshall G. 2003. Regional

621   heterothermy and conservation of core temperature in emperor penguins diving under sea ice.

622   Comp Biochem Physiol. Part A: Mol Int Physiol. 135: 477–487. doi: 10.1016/S1095-

623   6433(03)00133-8.

624   Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, *et al*. 2013. Ecological consequences

625   of sea-ice decline. Science 341: 519-524. doi: 10.1126/science.1235225.

626   R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for

627   Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

628   Rice KM, Walker EM Jr., Wu M, Gillette C, Blough ER. 2014. Environmental mercury and its toxic

629   effects. J Prev Med Public Health 47: 74-83. doi: 10.3961/jpmph.2014.47.2.74.

630   Richman SE, Lovvorn JR. 2011. Effects of air and water temperatures on resting metabolism of auklets

631   and other diving birds. Physiol Biochem Zool. 84: 31-332. doi:10.1086/660008.

632   Sibley R, Nott H, Fletcher D. 1990. Splitting behaviour into bouts. Anim Behav. 39: 63-69. doi:

633   10.1016/S0003-3472(05)80726-2.

634   Stager M, Senner NR, Tobalske BW, Cheviron ZA. 2020. Body temperature maintenance acclimates in a

635   winter-tenacious songbird. J Exp Biol. 223: jeb221853. doi: 10.1242/jeb.221853.

636 Ste-Marie E, Grémillet D, Fort J, Patterson A, Brisson-Curadeau É, Clairbaux M, Perret S, Speakman JR,

637 Elliott KH. 2022. Accelerating animal energetics: High dive costs in a small seabird disrupt the

638 dynamic body acceleration–energy expenditure relationship. J Exp Biol. 225: jeb243252. doi:

639 10.1242/jeb.243252.

640 Tapper S, Nocera JJ, Burness G. 2020 Experimental evidence that hyperthermia limits offspring

641 provisioning in a temperate- breeding bird. R Soc Open Sci. 7: 201589. doi: 10.1098/rsos.201589.

642 Torre-Bueno JR. 1976. Temperature regulation and heat dissipation during flight in birds. J Exp Biol. 65:

643 471-482. doi: 10.1242/jeb.65.2.471.

644 Wada H, Cristol DA, McNabb FMA, Hopkins WA. 2009. Suppressed adrenocortical responses an thyroid

645 hormone levels in birds near a mercury-contaminated river. Environ Sci Technol. 43: 6031-6038.

646 doi: 10.1021/es803707f.

647 Williams CL, Ponganis PJ. 2021 Diving physiology of marine mammals and birds: the development of

648 biologging techniques. Phil Trans R Soc. B 376: 20200211. doi: 10.1098/rstb.2020.0211.

649 Wilson RP, Pütz K, Grémillet D, Culik BM, Kierspel M, Regel J, Bost CA, Lage J, Cooper J. 1995.

650 Reliability of stomach temperature changes in determining feeding characteristics of seabirds. J

651 Exp Biol. 198: 1115–1135. doi: 10.1242/jeb.198.5.1115.

652 Wojczulanis-Jakubas K, Waż P, Jakubas D. 2020. Little auks under the midnight sun: diel activity rhythm

653 of a small diving seabird during the Arctic summer. Pol Res. 39: 3309. doi:

654 10.33265/polar.v39.3309.

655 Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of

656 semiparametric generalized linear models. J Roy Stat Soc B 73: 3-36. doi: 10.1111/j.1467-

657 9868.2010.00749.x.

658 Wood SN. 2017. Generalized Additive Models: An Introduction with R (2nd edition). Chapman and

659 Hall/CRC.