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1 **Mercury contamination challenges the behavioral response of a keystone species to Arctic climate**
2 **change**

3
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25

26 **Abstract:** Combined effects of multiple, climate change-associated stressors are of mounting concern,
27 especially in Arctic ecosystems. Elevated mercury (Hg) exposure in Arctic animals could affect behavioral
28 responses to changes in foraging landscapes caused by climate change, generating interactive effects on
29 behavior and population resilience. We investigated this hypothesis in little auks (*Alle alle*), a keystone
30 Arctic seabird. We compiled behavioral data for 44 birds across 5 years using accelerometers, while also
31 quantifying blood Hg and environmental conditions. Warm sea surface temperature (SST) and low sea ice
32 coverage (SIC) reshaped time activity budgets (TABs) and diving patterns, causing decreased resting,
33 increased flight, and longer dives. Mercury contamination was not associated with TABs. However,
34 highly contaminated birds lengthened inter-dive breaks when making long dives, suggesting Hg-induced
35 physiological limitations. As dive durations increased with warm SST, subtle toxicological effects
36 threaten to increasingly constrain diving and foraging efficiency as climate change progresses, with
37 ecosystem-wide repercussions.

38
39 **Synopsis:** Interactive effects of chemical contaminants and climate change are of mounting concern. Our
40 data suggest that subtle toxicological effects of mercury contamination might constrain animal behavioral
41 responses to climate change.

42
43 **Keywords:** Climate change, behavioral ecotoxicology, toxicant-induced climate change sensitivity,
44 multiple stressors, behavioral plasticity, mercury (Hg), diving behavior

45
46 **Introduction:** Global climate change is reconfiguring ecosystems, exposing organisms to multiple
47 interacting stressors, including thermal stress, resource redistribution, and altered pollutant exposure¹⁻⁴. A
48 pressing research priority involves understanding how multiple stressor interactions will affect biological
49 systems as climate change progresses⁵⁻⁷. In particular, mercury (Hg) contamination of marine ecosystems
50 is a persistent problem, which might be aggravated by altered Hg cycling in warming oceans⁸⁻¹⁰. Thus,
51 amplified toxicological effects of Hg exposure threaten to impair organismal resiliency to other climate

52 change-associated stressors¹¹⁻¹³, especially by affecting patterns of physiological and behavioral plasticity
53 whereby animals adjust to environmental variability¹⁴⁻¹⁷. Indeed, in its highly toxic methylated form
54 (methylmercury, MeHg), Hg acts as a potent neurotoxin and endocrine disrupter, which can substantially
55 alter physiology, energetics and behavioral capacity^{18,19}. Thus, Hg exposure has the potential to
56 exacerbate declines in behavioral performance under challenging environmental conditions (e.g. resource
57 limitation, predation risk), making behavioral reaction norms steeper and generating synergistic
58 effects^{14,20,21}. For example, Hg-exposed zebra finch (*Taeniopygia guttata*) increased foraging latency
59 under predation risk more than controls, with implications for energy intake²⁰. Concomitantly, Hg
60 contamination might inhibit behavioral adjustments, canalizing reaction norms. For instance, Hg exposure
61 can cause anemia and lower haemoglobin's oxygen carrying capacity, which might constrain diving
62 behavior in aquatic avian and mammalian predators faced with shifting prey distributions²².

63 The Arctic marine biota is vulnerable to joint effects of climate change and environmental Hg
64 contamination, such that the Arctic presents an important arena for studying how Hg exposure might
65 affect animal resiliency to climate change^{23,24}. The Arctic is warming > 3 times faster than other regions,
66 causing cascading effects on ecosystem structure⁴. For example, warming sea surface temperature (SST)
67 and drastic reductions in summer sea ice coverage (SIC) are reconfiguring foraging landscapes, leading to
68 behavioral and bioenergetic challenges²⁵⁻²⁸. Moreover, effects of climate change on the cryosphere and
69 biochemical cycling are altering contaminant exposure patterns, with rising Hg contamination in some
70 Arctic seabird and marine mammal populations presenting a special concern^{24,29-31}.

71 We used a keystone Arctic seabird, the little auk (dovekie, *Alle alle*), as a model species to explore
72 whether effects of Hg exposure on behavioral plasticity could underlie interactive effects of Hg
73 contamination and other climate change-associated stressors on Arctic animals. Little auks are the most
74 abundant seabird in the North Atlantic (~30-40 million breeding pairs globally), and act as ecosystem
75 engineers by transferring nutrients between marine and terrestrial ecosystems³². Energy-rich sea ice-
76 associated copepods upon which little auks specialize are declining with climate change, and smaller
77 Atlantic species moving northward, altering the little auk's resource base^{27,33,34}. Little auks exhibit high

78 flight and dive costs and operate close to maximum energy capacity, rendering them vulnerable to
79 energetic stress^{35,36}. Behavioral plasticity could buffer little auks, and ecosystems they underpin, against
80 climate change¹⁵. However, Hg exposure in little auks from East Greenland has risen concurrent with
81 climate change, threatening to impair behavioral plasticity and reproductive performance^{33,37}.

82 We leveraged temporal variation in environmental conditions across five years at a little auk colony in
83 East Greenland combined with advanced biologging techniques (triaxial accelerometry) and individual-
84 level Hg contamination measurements to test two hypotheses: (1) Warm oceanic conditions (high sea
85 surface temperature (SST), low SIC) affect little auk time activity budgets (TABs), increasing
86 energetically expensive flying and diving, and altering behavioral performance traits (flight and dive
87 durations); and (2) Mercury exposure exacerbates or inhibits changes in TABs, and finer scale
88 adjustments of behavioral performance traits, such as adjustments of dive duration to prey distributions³³.
89 Effects of Hg exposure on behavioral plasticity could constitute a mechanism driving multiple stressor
90 interactive effects by altering little auks' resiliency to climate change, which given the species' keystone
91 status, could have reverberating effects throughout Arctic ecosystems.

92 **Methods**

93 *Field methods:* We studied little auks at a colony at Ukaleqarteq (Kap Høegh; 70°44'N, 21°35'W), East
94 Greenland, during the breeding season (June-August, 2017-2021). The East Greenland Current transports
95 Arctic waters southward past Ukaleqarteq, promoting favourable foraging conditions for little auks, but
96 SST and SIC vary interannually, and climate change is increasingly elevating SST and reducing SIC^{29,33}.
97 Little auks nest under rocks, often in accessible locations. The sexes are of similar size and contribute
98 equally to parental care^{38,39}. Thus we did not distinguish between the sexes.

99 We equipped little auks with accelerometers (Axy4, Technosmart, 25 x 10 x 5 mm, 3.0 g, including
100 tape used for attachment, < 2% body mass) to derive records of TABs and behavioral performance traits
101 (dive/flight duration). During each season (July 19 to August 5, 2017-2021), we deployed accelerometers
102 during chick rearing, beginning when chicks were ~3-6 days old, as estimated by size⁴⁰ or determined via

103 hatching date. Sample sizes per year were 17, 7, 20, 11, and 7 across 2017-2021. We captured birds near
104 nests and secured accelerometers to ventral feathers using tesa® tape. Handling time was kept to a
105 minimum at the time of accelerometer deployment to limit effects on behavioral patterns. Birds were
106 recaptured within 3-11 days. Occasionally, shorter datasets (0.5-2 days) were obtained due to battery
107 difficulties. Data < 3/4th day (18 hrs) in duration (one dataset from 2021, 13 hr in duration, containing 132
108 dives) were not used in analyses of TABs, but were used when analysing other behavioral traits
109 (proportion deep diving, dive and inter-dive durations; see below). Removing this short dataset from the
110 analysis did not substantially alter results involving diving behavior. At recapture, we obtained small
111 blood samples (~0.2 mL) via brachial venepuncture for Hg analysis.

112

113 ***Determining behavioral traits from accelerometer data:*** Acceleration was logged in three dimensions at
114 50 Hz, with X corresponding to surge (back to front), Y to sway (side to side), and Z to heave (dorsal to
115 ventral). Temperature was logged at 0.2 Hz. We used Igor Pro 9.0 (WaveMetrics, Inc., Lake Oswego,
116 OR, USA) combined with Ethographer 2.05⁴¹ to process data and classify behaviors. In brief, acceleration
117 waves (data vectors measured at equal intervals) in all dimensions were smoothed using a rolling
118 algorithm (1 sec sliding window) in Igor, to extract gravitational acceleration. We calculated body pitch
119 using the formula: $\text{atan}(XW_B / (\text{sqrt}(YW_B^2 + ZW_B^2))) \times (180/\pi)$, and vectorial dynamic body
120 acceleration (VDBA) using the formula: $\text{sqrt}((XW_B-XW)^2+(YW_B-YW)^2+(ZW_B-ZW)^2)$, where
121 XW_B , YW_B and ZW_B are smoothed acceleration waves^{42,43}. We applied continuous wavelet
122 transformation to Z dimension waves to derive dominant wing beat frequency across time (1 Hz
123 resolution). We applied K-mean cluster analysis to dominant frequency waves, using four clusters, which
124 resulted in clusters corresponding to flying (~10-11 Hz), descending dives (~3.5-4.5 Hz), rest (~0 Hz),
125 and intermediate activity (~0-3.5 Hz). These values are consistent with previous work in little auks³⁶.

126 We wrote custom functions in Igor to classify behavior, using cluster analysis output, pitch, VDBA
127 and temperature. Flying was identified based on wing beat frequency of ~10-11 Hz. Dives started when

128 wing beat frequency was ~ 3.5 - 4.5 Hz and pitch was between -10 and -30° , and ended when pitch
129 increased to $> 40^\circ$ and then returned to zero at the water surface. We subdivided dives into deep dives,
130 wherein the descent phase with high wing beat frequency lasted > 5 seconds, and shallower dives,
131 wherein this phase lasted ≤ 5 seconds. Histograms revealed that these criteria captured a bimodal
132 distribution in dive durations. We calculated proportion of time deep versus shallower diving (hereafter,
133 proportion deep diving) as a metric of variation in foraging behavior. Time resting at the colony was
134 identified via absence of wing beat and elevated temperature ($> \sim 17^\circ\text{C}$), following a period of flight.
135 Time resting on sea ice was classified based on initial high pitch, indicating standing, absence of wing
136 beat, and elevated temperature (lower than for colony; ~ 12 - 16°C ; Fig. S1). Birds were classed as resting
137 on water based on low wing beat, low temperature ($> \sim 10^\circ\text{C}$), and absence of classification into another
138 category. We adjusted temperature and pitch ranges associated with behaviors depending on positioning
139 of accelerometers on individuals, with pitch standardized to zero during flight. We calculated TABs
140 (flying, resting at colony, on ice, diving, on water) across each accelerometer dataset's duration (Fig. S1),
141 rather than daily TABs, as Arctic breeding little auks are not constrained by daily light-dark cycles, and
142 lack circadian rhythms in behavior⁴⁴.

143 We also used accelerometer data to determine durations of foraging trips, dives, inter-dive intervals,
144 and flights, proportion time spent flying during foraging trips versus around the colony (hereafter,
145 proportion foraging flight), and chick provisioning rates. Breeding little auks display a dual foraging
146 strategy, with short trips used for provisioning chicks and longer trips for self-maintenance. We assumed
147 that short and long trips derive from two log-normal distributions⁴⁵. We log-transformed trip duration, and
148 used K-mean clustering in R (R Core 2021) to group foraging trips into two categories. The cutoff value
149 separating short and long trips was 3.9 hrs., which is lower than previously published values (~ 5.5 - 6
150 hrs.)^{46,47}. However, we preferred to use the value deriving from our dataset. We determined whether time
151 on the water surface was part of a dive bout (inter-dive interval) using the standard classification method
152 in R package *diveMove*⁴⁸. The bout ending criteria was 308 sec, and we assumed dives were ≤ 120 sec³⁶.

153 Thus, inter-dive intervals were defined as periods between dives ≤ 308 sec. Dive and inter-dive durations
154 can be interdependent⁴⁹, and might be constrained by contamination-linked physiological changes²². Thus,
155 we were interested in whether interrelationships between dive- and inter-dive durations were altered in
156 Hg-contaminated birds. We determined proportion of foraging flight by classifying flights embedded
157 within periods of resting at the colony as colony-based, and other flight as foraging-based, and taking the
158 quotient (foraging / colony-based flight). We estimated chick provisioning trips per day as the number of
159 colony visits ≥ 30 secs long (minimum time to feed chicks) that proceeded a foraging trip containing ≥ 5
160 dives. Video-recording data from accelerometer-equipped birds showed that colony visits fulfilling these
161 criteria were invariably associated with birds returning with a full gular pouch and feeding the chick.

162

163 ***Mercury contamination:*** Blood samples were centrifuged for 10 min at 3500 rpm, and red blood cells
164 (RBCs) stored in 70% ethanol pending analysis. RBCs were later freeze-dried for 48 hrs and
165 homogenized, after which total Hg concentrations were measured using an advanced Hg analyser
166 spectrophotometer (Altec AMA 254) at the Littoral Environnement et Sociétés (LIENSs) laboratory, La
167 Rochelle University⁵⁰. Mercury in avian blood consists primarily of MeHg ($> 90\%$)^{51,52}. Thus, total blood
168 Hg provides a good proxy for MeHg exposure. Two or more Hg measurements were taken per bird, using
169 small aliquots of dried RBCs (~ 1.5 -5 ng), until standard deviation was $< 10\%$. We regularly measured a
170 certified reference material (CRM; Lobster Hepatopancreas Tort-3; NRC, Canada; Hg concentration of
171 0.292 ± 0.022 $\mu\text{g/g}$ dry weight (dw)), and ran blanks before each session. The detection limit was 0.005
172 $\mu\text{g/g}$ and Tort-3 measurements (mean \pm SD) averaged 0.306 ± 0.004 $\mu\text{g/g}$. Mercury concentrations were
173 not available for 2017, hence analyses involving Hg do not include this year.

174 Our Hg measurements derived from dried RBCs, rather than whole blood. Thus, for comparison to
175 toxicological thresholds for birds, which have been formulated for measurements taken on whole blood
176 (wet weight (ww)), we used the equation recommended by Ackerman et al. (2016)⁵³ to convert Hg
177 concentrations in dried RBCs to whole blood (ww) equivalents. Namely, we assumed a blood moisture

178 content of 79%, and thus converted from dried RBC concentrations (dw) to whole blood (ww) equivalents
179 by multiplying the concentrations measured in RBCs by 0.21.

180

181 ***Sea surface temperature (SST) and sea ice coverage (SIC):*** We focused on relationships between SST
182 and SIC and behavior, as these variables strongly affect foraging conditions for little auks^{27,33,54}. We
183 determined SST within the little auk's primary foraging range at Ukaleqarteq, determined by GPS
184 tracking⁵⁵, using the National Oceanic and Atmospheric Administration's interpolated SST (OISST) high
185 resolution daily dataset (1/4° global grid;
186 <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>). The foraging range was encompassed
187 by -21.57° longitude west, -17.47° longitude east, 69.8° latitude south, and 71.65° latitude north, and
188 comprised an ~160 × 200 km area. We extracted daily SST across this area during the chick rearing
189 period, across all days of accelerometer deployment. We averaged daily values across the foraging range
190 and each day of accelerometer deployment for use in analyses.

191 SIC data were downloaded from the University of Bremen's Sea Ice Remote Sensing database
192 (<https://seaice.uni-bremen.de/sea-ice-concentration/amsre-amsr2/>). Data derived from brightness
193 temperature measurements from the Advanced Microwave Scanning Radiometer 2 (ASMR2) sensor,
194 mounted aboard the JAXA satellite "Shizuku" (GCOM-W1). The ASI algorithm permits derivation of
195 SIC by differences between brightness temperatures at 89 GHz and polarization, with atmospheric
196 corrections⁵⁶. We gridded data on a polar stereographic grid through near neighbor interpolation with
197 3.125 km resolution. We extracted daily SIC values, and derived averages from data spanning the
198 foraging range and days of accelerometer deployment, as for SST.

199 **Statistical Analysis:** We used R 4.1.2⁵⁷ to process and analyze data. We performed ANOVAs to compare
200 SST, SIC and Hg concentrations (log transformed) among years, and R package *emmeans* for *post-hoc*
201 comparisons (Tukey method)⁵⁸. We used linear mixed effect models (LMMs) with Satterthwaite

202 approximations for degrees of freedom and year as a random effect to assess whether blood Hg varied
203 with SST/SIC (R packages *lme4*, *lmerTest*)^{59,60}.

204 We analyzed TABs using Dirichlet (mixed) models fit in JAGS, via R2jags^{61,62}. The Dirichlet
205 distribution is a multivariate generalization of the beta distribution, suitable for multivariate
206 compositional data⁶³. JAGS implements Bayesian models via Markov Chain Monte Carlo (MCMC)
207 simulation. We ran four chains simultaneously with 50,000 repetitions, burn in of 25,000, thinning of 25,
208 and vague priors. All estimated parameters had an Rhat value of ~ 1 , indicating convergence. We first
209 compared TABs among years (fixed effect), with predicted differences determined as derived quantities.
210 We then used Dirichlet mixed models, with year as a random effect, to explore relationships between
211 SST, SIC (log transformed), and TABs. We assessed effects of Hg within the year-comparison (fixed
212 effect) model, and included an interaction between Hg and SST/SIC in the mixed model. Data were
213 transformed using the *DirichletReg* package prior to analysis to avoid zeros⁶⁴. We analyzed proportion
214 deep diving and proportion foraging flight using beta regression (mixed) models in R2jags, and the same
215 approach as above. Predicted differences and parameter estimates from models fit in R2jags were
216 considered significant when 95% credible intervals (CIs) did not cross zero. We used graphical inspection
217 and deviance information criterion (DIC) to assess model fit.

218 We analyzed among year variation in foraging trip and flight durations (per trip) using LMMs and
219 *emmeans*, with bird identity as a random effect (multiple trips per individual). Long and short trips were
220 analyzed separately. We used LMMs to analyze effects of SST/SIC, Hg and interactions on these
221 variables, with bird identity and year as random effects. The same analyses, but without repeated
222 measures on individuals, were performed for maximum continuous flight duration, deep dive duration,
223 and inter-dive duration (individual-level averages). We included interactions between Hg and inter-dive
224 or dive durations in models involving diving behavior, as dive and inter-dive durations can be
225 interdependent⁴⁹. We also performed a model predicting deep dive duration from the interaction between
226 foraging trip duration and SST/SIC, to assess the hypothesis that birds reach colder, more profitable
227 waters, in which diving behavior could differ, on longer trips. Individual identity was a random effect.

228 **Results**

229 **Variation in oceanic conditions and Hg contamination:** Across years, SST experienced by little auks
230 during accelerometer deployment within their primary foraging range averaged (mean \pm SE) $2.20 \pm$
231 0.224°C (range $-0.932, 7.416^\circ\text{C}$), and SIC averaged $3.33 \pm 0.867\%$ (range: 0.016-14.812 %). SST ($F_{4,57} =$
232 $43.66, P < 0.001$) and SIC ($F_{4,57} = 36.84, P < 0.001$) varied among years, with SST warmer and SIC
233 lower in 2018 and 2021 (Table 1). Blood Hg averaged $1.088 \pm 0.039 \mu\text{g/g dw}$ (range: 0.579-1.745 $\mu\text{g/g}$
234 dw), or, for comparison to toxicological benchmarks, $\sim 0.228 \mu\text{g/g ww}$ (range: 0.121-0.366 $\mu\text{g/g ww}$),
235 assuming blood moisture content of 79%⁶⁴. Blood Hg ($\mu\text{g/g}$) concentrations varied somewhat among
236 years ($F_{3,40} = 7.706, P < 0.001$) (Table 1).

237

238 **Warm oceanic conditions affect TABs and foraging patterns:** Variation in oceanic conditions (SST,
239 SIC) among years correlated with reshaping of TABs. In high SST-low SIC years (2018, 2021), little auks
240 were predicted to spend as much as 11.7% (2.7%, 21.1%) more time flying, 23.2% (12.8%, 32.9%) more
241 time on water, 21.4% (14.8%, 28.1%) less time resting on ice, and 27.6% (21.9%, 32.6%) less time
242 resting at the colony relative to in cold years (Fig. 1a-e., Fig. S2). However, time resting at the colony was
243 also low in the coldest year of 2020 (Fig. 1b). Percent time diving was consistent across years, at 15-19%
244 (Fig. 1d).

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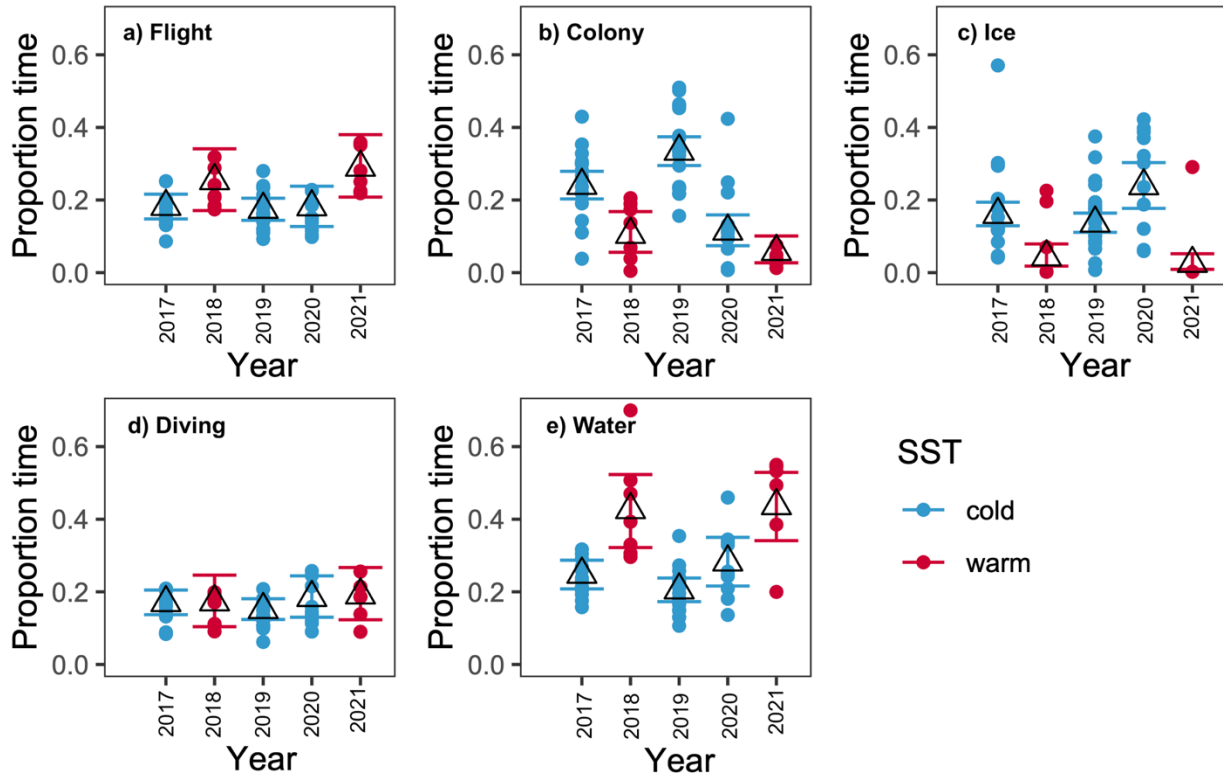
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254 **Table 1.** Variation in a) sea surface temperature (SST; °C) and b) sea ice coverage (SIC; %), and c) blood
 255 mercury (Hg) concentrations (µg/g dw), experienced by little auks at Ukaleqarteq, East Greenland,
 256 summarized across study years. We quantified values for environmental variables (SST, SIC) on a per-
 257 individual basis, depending on the period of accelerometer deployment.

a) SST				
Year	Mean ± SE	95% CI	Range	N
2017	2.472 ± 0.245	1.981, 2.964	3.312, 2.585	17
2018	3.615 ± 0.382	2.850, 4.381	3.544, 4.038	7
2019	1.415 ± 0.226	0.963, 1.868	0.318, 3.353	20
2020	-0.055 ± 0.305	-0.666, 0.555	-0.932, 0.675	11
2021	5.886 ± 0.382	5.120, 6.651	4.738, 7.416	7
Overall	2.20 ± 0.224	1.75, 2.64	-0.932, 7.416	62
b) SIC				
2017	1.820 ± 0.497	1.052, 3.146	1.589, 2.027	17
2018	0.081 ± 0.034	0.034, 0.190	0.057, 0.263	7
2019	1.192 ± 0.300	0.719, 1.974	0.096, 4.736	20
2020	10.058 ± 3.417	5.093, 19.861	5.165, 14.812	11
2021	0.035 ± 0.015	0.015, 0.083	0.016, 0.078	7
Overall	3.33 ± 0.867	2.48, 41.8	0.016, 14.812	62
c) Blood Hg				
2018	1.210 ± 0.096	1.031, 1.420	0.940-1.488	7
2019	0.916 ± 0.044	0.831, 1.010	0.579-1.627	19
2020	1.291 ± 0.082	1.136, 1.470	0.993-1.745	11
2021	1.193 ± 0.094	1.016, 1.400	1.102-1.272	7
Overall	1.088 ± 0.039	1.013, 1.169	0.579-1.745	44

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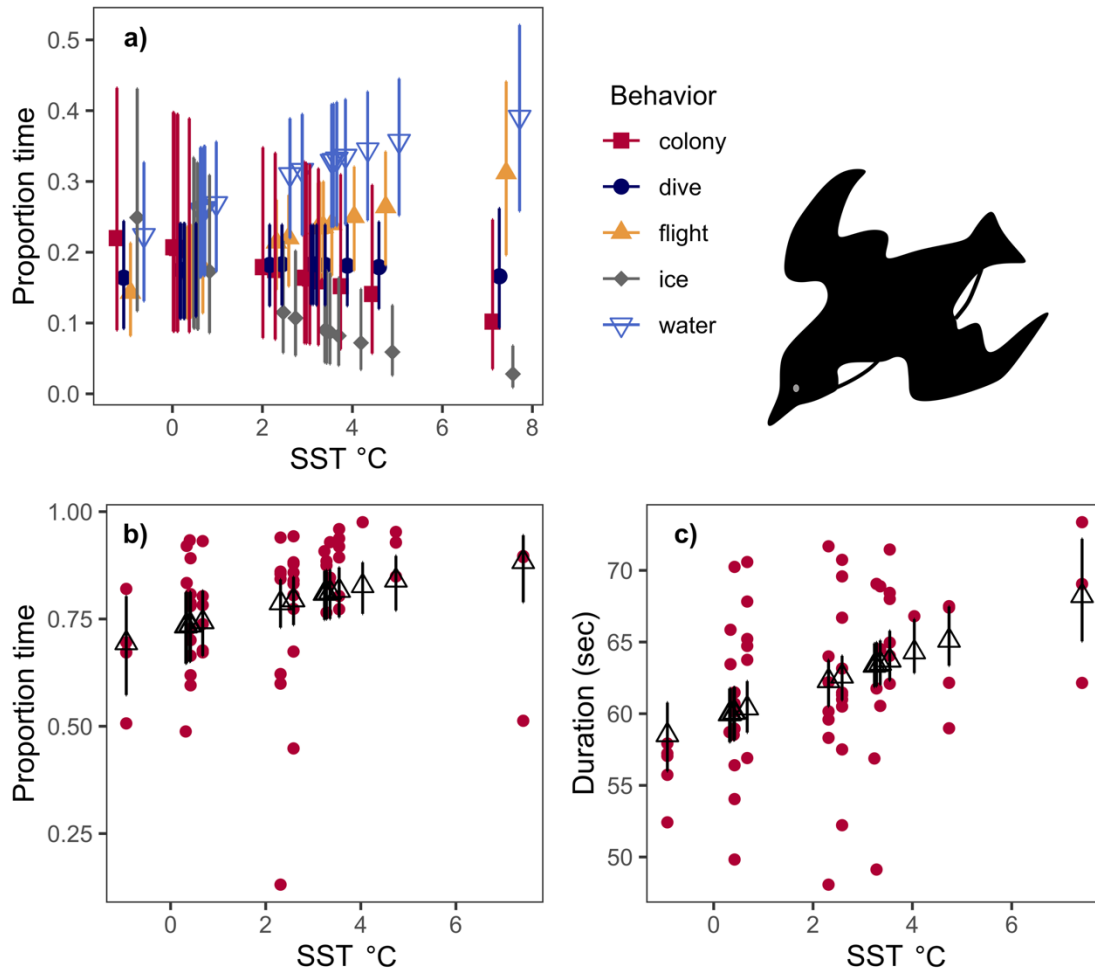
Figure 1. Little auk TABs across years at Ukaleqarteq, East Greenland. Relatively cold (blue; average SST < 2.5°C) and warm (red; average SST > 3.5°C) SST years are differentiated by color to facilitate visualization of differences in behavior associated with warmer conditions. Open triangles are predicted means and error bars represent 95% CIs. Colored points are observed values.

Dirichlet mixed models substantiated strong effects of SST and SIC on TABs. Beta coefficient estimates for SST (and SIC) had 95% CIs not crossing zero for time resting on ice (-0.679 (-0.998, -0.341)) and at the colony (-0.329 (-0.626, -0.045)) (Table S1). Predicted values for other behavioral categories were also affected by SST and SIC, as predictions for behavioral categories are interdependent (Fig. 2a). Time resting on ice was predicted to drop from ~25% to < 3%, time resting at the colony decline (~22 to 10%), time flying (~14 to 30%) and on water (~24 to 38%) increase, and diving time remain constant (~17-18%), as SST increased from < 0°C to > 7°C (Fig. 2a).

272 Little auk foraging trip and flight patterns were altered under warm conditions, with long trips
273 primarily affected (Fig. S3a-d; Table S2-S6). Long trip duration ($F_{4,49} = 5.022, P < 0.001$), flight time per
274 long trip ($F_{4,56} = 6.801, P < 0.001$), and maximum continuous flight duration ($F_{4,56} = 3.321, P = 0.016$)
275 were greatest during high SST years (Table S2-S4, Fig. S3a, b). In the warmest year (2021), long trips
276 lasted 27.5 hrs. (20.4, 37.1), little auks flew 7.76 hrs. (5.43, 11.09) during long trips, and maximum
277 continuous flight duration was 2.23 hrs. (1.58, 2.88), compared to 14.4 hrs. (12.3, 16.9), 3.12 hrs. (2.56,
278 3.80), and 1.04 hrs. (0.563, 1.51) in 2019. In mixed models, flight time per long trip ($\beta \pm SE = 0.307 \pm$
279 $0.068, t_{10} = 4.511, P < 0.001$) and maximum continuous flight duration ($\beta \pm SE = 0.255 \pm 0.106, t_{10} =$
280 $2.395, P = 0.039$) increased with SST, and long trip duration tended to increase ($\beta \pm SE = 0.122 \pm 0.066,$
281 $t_{11} = 1.857, P = 0.090$). Little auks spent more time flying around the colony in cold years, with predicted
282 differences as high as 11.2% (7.7%, 15.1%), reflecting higher colony attendance (Fig. S3e, Fig. S4a).
283 However, in mixed models, there was no overall effect of SST (0.022 (-0.332, 0.376)) or SIC (-0.037 (-
284 0.363, 0.276)) on proportion foraging flight.

285 Diving behavior changed with oceanic conditions. Little auks were predicted to spend as much as
286 15.7% (4.2, 26.8) more time deep rather than shallow diving in high SST years (Fig. S3f, Fig. S4b). In
287 mixed models, beta coefficient estimates were 0.293 (0.025, 0.555) and -0.143 (-0.246, -0.037) for SST
288 and SIC, respectively, with proportion deep diving predicted to increase from 69.4% (57.3, 80.3) to
289 88.3% (78.9, 94.5) under the lowest (-0.9°C) versus highest (7.4°C) SST (Fig. 2b). Deep dive ($F_6 = 15.01,$
290 $P < 0.001$) and inter-dive duration ($F_6 = 9.305, P < 0.001$) were longest in high SST years (Table S7-S8;
291 Fig. S3g, h), although *post-hoc* comparisons were non-significant. However, the mixed model indicated
292 that little auks made longer dives when SST was high ($\beta \pm SE = 2.194 \pm 0.797, t_{41} = 3.246, P = 0.002$; Fig.
293 2c). Moreover, foraging trip duration interacted with SST to predict deep dive duration, with dives shorter
294 on longer foraging trips when SST in the primary foraging range was high ($\beta \pm SE = -0.014 \pm 0.004, t_{397}$
295 $= -2.966, P = 0.003$).

296 Chick provisioning rates (feeds/day) varied among years ($F_4=2.929$, $P = 0.029$), tending to be highest
 297 in cold years (e.g. 2019: (2.580 (2.114, 3.040)), 2020: 2.810 (2.116, 3.500)), and lowest in warm years
 298 (e.g. 2021: 1.540 (0.688, 2.390); Fig. S3i, Table S9). However, *post-hoc* comparisons were non-
 299 significant ($P > 0.169$), and effects of SST ($\beta \pm SE = -0.131 \pm 0.172$, $t_5 = -0.762$, $P = 0.477$) and SIC ($\beta \pm$
 300 $SE = 0.101 \pm 0.081$, $t_{15} = 1.239$, $P = 0.234$) on provisioning rates were non-significant in mixed models.

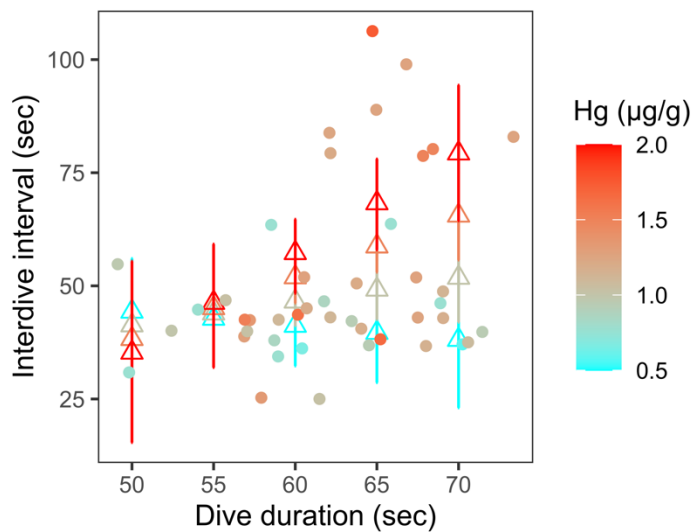


301
 302 **Figure 2.** Little auk a) TABs (points staggered to facilitate viewing), b) proportion time deep versus
 303 shallow diving, and c) deep dive duration at Ukaleqarteq, East Greenland, as a function of increasing
 304 SST, with year as a random effect. Shapes at the center of error bars are predicted means, and error bars
 305 represent 95% credible a, b) or confidence c) intervals. Circular red points in b) and c) are observed
 306 values. Confidence intervals around LMM predictions were derived using bootstrapping.

307 ***Mercury concentrations unrelated to TABs, but associated with dive bout patterning***

308 TABs did not vary with blood Hg concentrations, irrespective of oceanic conditions. Beta coefficient
309 estimates for Hg had 95% CIs overlapping zero in the year-comparison model (Fig. S5). In the mixed
310 model, there was no statistically significant effect of Hg on TABs, additively or in interaction with SST,
311 with 95% CIs overlapping zero, and DICs higher than in models including SST alone. Hg concentrations
312 were unrelated to foraging trip and flight durations ($P > 0.20$), proportion foraging-based flight (0.003 (-
313 0.331, 0.357)), and proportion deep diving (1.027 (-2.663, 4.399)). Little auk deep dive duration was
314 unrelated to Hg concentrations ($\beta \pm SE = 0.637 \pm 0.797$, $t_{41} = 0.800$, $P = 0.428$), and interaction terms
315 involving SST and SIC were non-significant ($P > 0.05$).

316



322 **Figure 3.** Interaction between dive duration and Hg concentrations in predicting inter-dive durations
323 between deep dives for little auks at Ukaleqarteq. Open triangles are predicted values with 95% CIs for
324 birds with Hg concentrations spanning the observed range. Closed points are observed values. Birds with
325 higher Hg concentrations lengthened inter-dive intervals with dive duration, whereas those with lower Hg
326 concentrations did not. Confidence intervals around LMM predictions were derived using bootstrapping.

327

328 However, little auks with higher blood Hg concentrations increased inter-dive interval duration with
329 dive duration more than less contaminated individuals, as reflected by a significant interaction between
330 dive duration and Hg in predicting inter-dive interval duration ($\beta \pm SE = 6.704 \pm 2.991$, $t_{40} = 2.241$, $P =$
331 0.031; Fig. 3). The same pattern held when analyzing observations of every dive (and inter-dive) made by
332 individuals, in sequence, rather than means (interaction: $\beta \pm SE = 1.980 \pm 0.244$, $t_{32350} = 8.120$, $P <$
333 0.001).

334 **Discussion:** Multiple stressor effects involving exposure to contaminants, such as Hg, are attracting
335 growing concern in the context of rapid climate change^{1,5,11}. Yet, understanding of mechanisms
336 underlying such effects remains limited. We addressed this deficit by exploring joint effects of climate
337 change-associated environmental variables and Hg contamination on a keystone Arctic seabird's
338 behavioral ecology. We hypothesized that warm oceanic conditions induce costly behavioral changes, and
339 that Hg exposure might exacerbate or inhibit behavioral responses, generating interactive effects. Below
340 we discuss evidence for these hypotheses, and implications of our findings.

341 *TABs and behavioral performance demands under warm conditions:* Climate change is increasingly
342 exposing little auks to warm oceanic conditions, which alter resource distribution³³. Our data demonstrate
343 that warm conditions reconfigure TABs in these sea-ice adapted seabirds, reducing time resting at the
344 colony and on ice, and increasing time in flight and on water. Accelerometer data revealed that sea ice
345 serves as an important resting substrate for little auks at Ukaleqarteq in years with substantial SIC. Thus,
346 loss of ice will likely reduce rest quality for little auks at sea, with energetic and health implications^{65,66}.
347 Indeed, thermoregulatory costs are elevated for seabirds resting in water⁶⁵, although warming SST may
348 reduce these costs⁶⁷. A previous study could not differentiate energetic costs of resting on water versus
349 land or ice for little auks, but did not differentiate land versus ice³⁶. Energetic costs of resting on land at
350 the colony might be elevated by anti-predator vigilance⁶⁸. Little auks also reduced time resting at and
351 flying around the colony during warm periods, further reducing rest, and altering colony-based social
352 dynamics, which are critically important in many seabirds^{69,70}.

353 As rest and social time decreased, foraging and behavioral performance demands increased. Little auks
354 spent more time flying and made longer continuous flights under warmer conditions, suggesting an
355 increase in foraging range. Indeed, even when there was virtually no sea ice within the primary foraging
356 range around Ukaleqarteq, tagged birds spent some time on ice, with ice reached via prolonged flight (> 2
357 hrs.). Studies at other colonies suggest that little auks can fly > 100 km to reach profitable foraging areas
358 at marginal sea ice zones when foraging conditions are poor near colonies⁷¹, and similar increases in
359 foraging range also occurs in other seabird species⁷². Increased foraging range can maintain energy
360 intake, but decreases net energy return for central place foragers. Thus, foraging range commonly
361 correlates negatively with breeding performance in central place foragers, including little auks^{73,74}.
362 Accordingly, little auk chick provisioning rates at Ukaleqarteq tended to decline with warm conditions,
363 when flight times were longest. Little auks at Ukaleqarteq also increased proportion deep diving and dive
364 duration with warm SST, likely reflecting altered copepod distribution³³. Previous analyses suggest that
365 energetic costs do not scale to dive duration in little auks³⁶, but utilized small sample sizes and did not
366 consider dive depth, which could make identifying energetic patterns difficult. Longer dives might
367 challenge physiological limitations by approaching aerobic dive capacity^{75,76}. Thus, results suggest that
368 warm conditions force little auks at Ukaleqarteq to adopt more energetically and physiologically
369 demanding behavior, with rest reduced, activity increased, and behavioral performance demands
370 intensified, at diminishing return.

371 *Behavioral correlates of Hg contamination:* We hypothesized that Hg exposure might reduce the
372 capacity of birds to maintain behavioral performance or upregulate costly behavior given altered foraging
373 landscapes under warm conditions. To the contrary, little auk Hg concentrations were not related to
374 TABs. When compared to toxicological benchmarks for avian blood⁵², little auk blood Hg concentrations
375 at Ukaleqarteq (which fall in the range of 0.2-1.0 µg/g ww) suggest low toxicological risk, despite recent
376 increases in Hg exposure, which could explain this result. However, a recent study on thick-billed murres
377 (*Uria lomvia*) found interrelationships between thyroid hormone levels, time spent diving and Hg
378 exposure with only slightly higher total blood Hg (mean ± SE = 1.51 ± 0.05 µg/g dw, or ~0.31 µg/g ww,

379 range: 0.81-2.74 $\mu\text{g/g}$ dw, or \sim 0.17-0.36 $\mu\text{g/g}$ ww). Murres with elevated blood Hg showed altered
380 triiodothyronine (T3) levels when sea ice break up was early, and murres were likely stressed due to poor
381 foraging conditions, but not given more usual ice conditions. In turn, elevated T3 levels were associated
382 with reduced time diving, suggesting that thyroidal dysregulation in Hg exposed birds could affect
383 activity budgets under stressful environmental conditions¹⁴.

384 Rather than affecting TABs, Hg exposure could alter behavioral performance traits or temporal
385 patterning of behavior. Little auks with higher Hg concentrations exhibited changes in dive bout
386 patterning, with inter-dive breaks lengthened when individuals were making long dives. Mercury
387 exposure might cause physiological impairments, such as decreased oxygen carrying capacity²², forcing
388 dive bout restructuring as birds approach aerobic dive capacity. Mercury can interfere with heme-proteins
389 including haemoglobin and myoglobin, which play critical roles in oxygen carrying capacity in blood and
390 muscles, respectively^{77,78}. Indeed, Hg contaminated common loons (*Gavia immer*) showed increased
391 diving frequency, concurrent with reduced dive duration, suggesting reduced aerobic dive capacity²². In
392 contrast, little auks with higher Hg maintained dive duration, but lengthened inter-dive breaks. Adjusting
393 inter-dive durations might allow Hg-contaminated birds to perform long dives despite physiological
394 impairments when long dives are essential to prey capture. However, lengthening breaks might eventually
395 reduce time underwater or resting outside of dive bouts, with implications for foraging efficiency,
396 digestion and recovery^{49,79,80}.

397 Effects of Hg contamination on little auk diving behavior are predicted to increase with warming
398 conditions. When SST was high and SIC low, little auks at Ukaleqarteq spent more time deep diving and
399 increased dive duration (Fig. 2b, c). Thus, as Hg-contaminated birds increased inter-dive durations when
400 making longer dives, Hg contamination might increasingly constrain diving patterns and foraging
401 efficiency as SST increases with climate change. Changes in Hg exposure with climate change might also
402 combine with foraging challenges to elevate toxicological effects on little auks and ecosystems they
403 underpin²⁴.

404 In conclusion, warm oceanic conditions affect TABs and finer scale behavior in little auks, a sea-ice
405 adapted Arctic seabird. Mercury exposure threatens to alter behavioral responses, generating climate
406 change-by-contamination interactive effects. Mercury contamination was not correlated with TABs.
407 However, birds with high Hg concentrations took longer inter-dive breaks when making long dives,
408 suggesting physiological constraint. A next step will be exploring the nature of this constraint, for
409 instance by measuring oxygen carrying capacity. As little auks engaged in longer dives given warm SST,
410 subtle behavioral effects of Hg-contamination threaten to increasingly constrain this keystone species'
411 foraging efficiency in a warming Arctic, with ecosystem-wide repercussions.

412

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433 **References**

434 ¹Noyes, P.D., McElwee, M.K., Miller, H.D., Clark, B.W., Van Tiem, L.A., Walcott, K.C., Erwin K.N.,
435 Levin, E.D. (2009) The toxicology of climate change: Environmental contaminants in a warming
436 world. *Environ Int.* 35:971–986. doi:10.1016/j.envint.2009.02.006.

437 ²Sherwood, S.C., Huber, M. (2010) An adaptability limit to climate change due to heat stress. *Proc Natl*
438 *Acad Sci USA.* 107:9552–9555. doi:10.1073/pnas.0913352107.

439 ³Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M., MacDougall A.S,
440 Tunney, T.D., McMeans, B.C. (2019) Food web rewiring in a changing world. *Nat Ecol Evol.*
441 3:345–354. doi:10.1038/s41559-018-0772-3.

442 ⁴IPCC. (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to
443 the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Masson-
444 Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y.,
445 Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock,
446 T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (eds.). Cambridge University Press.

447 ⁵Crain, C.M., Kroeker, K., Halpern, B.S. (2008) Interactive and cumulative effects of multiple human
448 stressors in marine systems. *Ecol Lett.* 11:1304-15. doi: 10.1111/j.1461-0248.2008.01253.x.

449 ⁶Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., Van den
450 Brink, P.J., De Laender, F., Stoks, R., Holmstrup, M., Matthaei, C.D., Monk, W.A., Penk, M.R.,
451 Leuzinger, S., Schaefer, R.B., Piggott, J.J. (2020) Towards a unified study of multiple stressors:
452 divisions and common goals across research disciplines. *Proc Roy Soc. B* 287:20200421.
453 doi:10.1098/rspb.2020.0421. Epub 2020.

454 ⁷Tekin, E., Diamant, E.S., Cruz-Loya, M., Enriquez, V., Singh, N., Savage, V.M., Yeh, P.J. (2020) Using
455 a newly introduced framework to measure ecological stressor interactions. *Ecol Lett.* 23:1391-
456 1403. doi:10.1111/ele.13533.

457 ⁸Cossa, D. (2013) Methylmercury manufacture. *Nature Geosci* 6:810–811. doi: 10.1038/ngeo1967.

458 ⁹Eagles-Smith, C.A., Silbergeld, E.K., Basu, N., Bustamante, P., Diaz-Barriga, F., Hopkins, W.A., Kidd,
459 K.A., Nyland, J.F. (2018) Modulators to mercury risk to wildlife and humans in the context of
460 rapid global change. *Ambio* 47:170–197.

461 ¹⁰Schartup, A.T., Thackray, C.P., Qureshi, A., Dassuncao, C., Gillespie, K., Hanke, A., Sunderland, E.M.
462 (2019) Climate change and overfishing increase neurotoxicant in marine predators. *Nature* 572:
463 648–650. doi:10.1038/s41586-019-1468-9.

464 ¹¹Hooper, M.J., Ankley, G.T., Cristol, D.A., Maryoung, L.A., Noyes, P.D., Pinkerton, K.E. (2013)
465 Interactions between chemical and climate stressors: A role for mechanistic toxicology in
466 assessing climate change risks. *Environ Toxicol Chemi.* 32:32–48. doi:10.1002/etc.2043.

467 ¹²Pirota, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J.O.,
468 Moore, M.J., Photopoulou, T., Rolland, R.M., Schwacke, L., Simmons, S.E., Southall, B.L.,
469 Tyack, P.L. (2022) Understanding the combined effects of multiple stressors: A new perspective
470 on a longstanding challenge. *Sci Tot Environ* 821: 153322. doi: 10.1016/j.scitotenv.2022.153322.

471 ¹³Turschwell, M.P., Connolly, S.R., Schäfer, R.B., De Laender, F., Campbell, M.D., Mantyka-Pringle, C.,
472 Jackson, M.C., Kattwinkel, M., Sievers, M., Ashauer, R., Côté, I.M., Connolly, R.M., van den
473 Brink, P.J., Brown, C.J. (2022) Interactive effects of multiple stressors vary with consumer
474 interactions, stressor dynamics and magnitude. *Ecol Lett.* 25:1483-1496. doi:10.1111/ele.14013.

475 ¹⁴Esparza, I., Elliott, K.H., Choy, E.S., Braune, B.M., Letcher, R.J., Patterson, A., Fernie, K.J. (2022)
476 Mercury, legacy and emerging POPs, and endocrine-behavioural linkages: Implications of Arctic
477 change in a diving seabird. *Environ Res.* 212:113190. doi:10.1016/j.envres.2022.113190.

478 ¹⁵Grémillet, D., Welcker, J., Karnovsky, N., Walkusz, W., Hall, M., Fort, J., Brown, Z., Speakman, J.R.,
479 Harding, A.M.A. 2012. Little auks buffer the impact of current Arctic climate change. *Mar Ecol*
480 *Prog Ser.* 454:197–206. doi:10.3354/meps09590.

481 ¹⁶Atwood, T.C., Peacock, E., McKinney, M.A., Lillie, K., Wilson, R., Douglas, D.C., Miller, S.,
482 Terletzky, P. (2016) Rapid environmental change drives increased land use by an arctic marine
483 predator. *PloS ONE* 11: e0155932. doi:10.1371/journal.pone.0155932.

484 ¹⁷Hall, L.E., Chalfoun, A.D. (2019) Behavioural plasticity modulates temperature-related constraints on
485 foraging time for a montane mammal. *J Anim Ecol.* 88: 363-375. doi:10.1111/1365-2656.12925.

486 ¹⁸Whitney, M.C., Cristol, D.A. (2018) Impacts of Sublethal Mercury Exposure on Birds: A Detailed
487 Review. *Rev Environ Contam Toxicol.* 244:113-163. doi:10.1007/398_2017_4.

488 ¹⁹Gerson, A.R., Cristol, D.A., Seewagen, C.L. (2019) Environmentally relevant methylmercury exposure
489 reduces the metabolic scope of a model songbird. *Environ Pollut.* 246: 790-796. doi:
490 10.1016/j.envpol.2018.12.072.

491 ²⁰Kobiela, M.E., Cristol, D.A., Swaddle, J.P. (2015) Risk-taking behaviours in zebra finches affected by
492 mercury exposure. *Anim Behav.* 103:153–160. doi:10.1016/j.anbehav.2015.02.024.

493 ²¹Bustnes, J.O., Bourgeon, S., Leat, E.H.K., Magnusdóttir, E., Strøm, H., Hanssen, S.A., Petersen A.,
494 Olafsdóttir, K., Borgå, K., Gabrielsen, G.W., Furness, R.W. (2015) Multiple stressors in a top
495 predator seabird: potential ecological consequences of environmental contaminants, population
496 health and breeding conditions. *PloS ONE* 10: e0131769. Doi:10.1371/journal.pone.0131769.

497 ²²Olsen, B., Evers, D., DeSorbo, C. (2000) Effect of methylated mercury on the diving frequency of the
498 common loon. *J Ecol Res.* 2:67–72.

499 ²³Krabbenhoft, D.P., Sunderland, E.M. (2013) Global Change and Mercury. *Science* 341:1457–1458.
500 doi:10.1126/science.1242838.

501 ²⁴AMAP. (2021) 2021 AMAP Mercury Assessment. Summary for Policy-makers. Arctic Monitoring and
502 Assessment Programme (AMAP), Tromsø, Norway. 16 pp.

503 ²⁵Eamer, J., Donaldson, G., Gaston, T., Kosobokova, K., Lárusson, K.F., Melnikov, I., Reist, J.D.,
504 Richardson, E., Staples, L., von Quillfeldt, C.H. (2013) Life linked to ice. A guide to sea-ice
505 associated biodiversity in this time of rapid change. Akureyri, Iceland: CAFF International
506 Secretariat. 115 p. (CAFF Assessment Series, Vol. 10).

507 ²⁶Davidson, S.C., Bohrer, G., Gurarie, E., LaPoint, S., Mahoney, P.J., Boelman, N.T., Eitel, J.U.H.,
508 Prugh, L.R., Vierling, L.A., Jennewein, J., Grier, E., Couriot, O., Kelly, A.P., Meddens, A.J.H.,
509 Oliver, R.Y., Kays, R., Wikelski, M., Aarvak, T., Ackerman, J.T., Alves, J.A., Bayne, E.,
510 Bedrosian, B., Belant, J.L., Berdahl, A.M., Berlin, A.M., Berteaux, D., Bêty, J., Boiko, D.,
511 Booms, T.L., Borg, B.L., Boutin, S., Boyd, W.S., Brides, K., Brown, S., Bulyuk, V.N., Burnham,
512 K.K., Cabot, D., Casazza, M., Christie, K., Craig, E.H., Davis, S.E., Davison, T., Demma, D.,
513 DeSorbo, C.R., Dixon, A., Domenech, R., Eichhorn, G., Elliott, K., Evenson, J.R., Exo, K.M.,
514 Ferguson, S.H., Fiedler, W., Fisk, A., Fort, J., Franke, A., Fuller, M.R., Garthe, S., Gauthier, G.,
515 Gilchrist, G., Glazov, P., Gray, C.E., Grémillet, D., Griffin, L., Hallworth, M.T., Harrison, A.L.,
516 Hennin, H.L., Hipfner, J.M., Hodson, J., Johnson, J.A., Joly, K., Jones, K., Katzner, T.E., Kidd,
517 J.W., Knight, E.C., Kochert, M.N., Kölzsch, A., Kruckenberg, H., Lagassé, B.J., Lai, S., Lamarre,
518 J.F., Lanctot, R.B., Larter, N.C., Latham, A.D.M., Latty, C.J., Lawler, J.P., Léandri-Breton, D.J.,
519 Lee, H., Lewis, S.B., Love, O.P., Madsen, J., Maftai, M., Mallory, M.L., Mangipane, B.,
520 Markovets, M.Y., Marra, P.P., McGuire, R., McIntyre, C.L., McKinnon, E.A., Miller, T.A.,
521 Moonen, S., Mu, T., Müskens, G.J.D.M., Ng, J., Nicholson, K.L., Øien, I.J., Overton, C., Owen,
522 P.A., Patterson, A., Petersen, A., Pokrovsky, I., Powell, L.L., Prieto, R., Quillfeldt, P., Rausch, J.,
523 Russell, K., Saalfeld, S.T., Schekkerman, H., Schmutz, J.A., Schwemmer, P., Seip, D.R.,
524 Shreading, A., Silva, M.A., Smith, B.W., Smith, F., Smith, J.P., Snell, K.R.S., Sokolov, A.,
525 Sokolov, V., Solovyeva, D.V., Sorum, M.S., Tertitski, G., Therrien, J.F., Thorup, K., Tibbitts,
526 T.L., Tulp, I., Uher-Koch, B.D., van Bemmelen, R.S.A., Van Wilgenburg, S., Von Duyke, A.L.,
527 Watson, J.L., Watts, B.D., Williams, J.A., Wilson, M.T., Wright, J.R., Yates, M.A., Yurkowski,
528 D.J., Žydelis, R., Hebblewhite, M. (2020) Ecological insights from three decades of animal

529 movement tracking across a changing Arctic. *Science* 370: 712-715. doi:
530 10.1126/science.abb7080. PMID: 33154141.

531 ²⁷Jakubas, D., Wojczulanis-Jakubas, K., Iliszko, L.M., Strøm, H., Stempniewicz, L. (2017) Habitat
532 foraging niche of a High Arctic zooplanktivorous seabird in a changing environment. *Sci Rep.*
533 7:16203. doi:10.1038/s41598-017-16589-7.

534 ²⁸Blanchet, M-A., Aars, J., Andersen, M., Routti, H. (2020) Space-use strategy affects energy
535 requirements in Barents Sea polar bears. *Mar Ecol Prog Ser.* 639: 1-19. doi: 10.3354/meps13290.

536 ²⁹Fort, J., Grémillet, D., Traisnel, G., Amélineau, F., Bustamante, P. (2016) Does temporal variation of
537 mercury levels in Arctic seabirds reflect changes in global environmental contamination, or a
538 modification of Arctic marine food web functioning? *Environ Pollut.* 211:382-8. doi:
539 10.1016/j.envpol.2015.12.061.

540 ³⁰Morris, A.D., Wilson, S.J., Fryer, R.J., Thomas, P.J., Hudelson, K., Andreassen, B., Blévin, P.,
541 Bustamante, P., Chastel, O., Christensen, G., Dietz, R., Evans, M., Evenset, A., Ferguson, S.H.,
542 Fort, J., Gamberg, M., Grémillet, D., Houde, M., Letcher, R.J., Loseto, L., Muir, D., Pinzone, M.,
543 Poste, A., Routti, H., Sonne, C., Stern, G., Rigét, F.F. (2022) Temporal trends of mercury in
544 Arctic biota: 10 more years of progress in Arctic monitoring. *Sci Tot Environ.* 839C:155803.
545 doi:10.1016/j.scitotenv.2022.155803.

546 ³¹Tartu, S., Blévin, P., Bustamante, P., Angelier, F., Bech, C., Bustnes, J.O., Chierici, M., Fransson, A.,
547 Gabrielsen, G.W., Goutte, A., Moe, B., Sauser, C., Sire, J., Barbraud, C., Chastel, O. (2022) A U-
548 turn for mercury concentrations over 20 years: how do environmental conditions affect exposure
549 in Arctic seabirds? *Environ Sci Technol.* 56:2443–2454. doi:10.1021/acs.est.1c07633.

550 ³²González-Bergonzoni, I., Johansen, K.L., Mosbech, A., Landkildehus, F., Jeppesen, E., Davidson, T.A.
551 (2017) Small birds, big effects: the little auk (*Alle alle*) transforms high Arctic ecosystems. *Proc*
552 *R Soc. B* 284:20162572. doi: 10.1098/rspb.2016.2572.

553 ³³Amélineau, F., Grémillet, D., Harding, A.M.A., Walkusz, W., Choquet, R., Fort, J. (2019) Arctic
554 climate change and pollution impact little auk foraging and fitness across a decade. *Sci Rep.*
555 9:1014. doi:10.1038/s41598-018-38042-z.

556 ³⁴Ershova, E.A., Kosobokova, K.N., Banas, N.S., Ellingsen, I., Niehoff, B., Hildebrandt, N., Hirche, H.J.
557 (2021) Sea ice decline drives biogeographical shifts of key Calanus species in the central Arctic
558 Ocean. *Glob Chang Biol.* 10:2128-2143. doi: 10.1111/gcb.15562.

559 ³⁵Gabrielsen, G.W., Taylor, J.R.E., Konarzewski, M., Mehlum, F. (1991) Field and laboratory metabolism
560 and thermoregulation in dovekies (Alle alle). *Auk* 108: 71–78. doi: 10.1093/auk/108.1.71.

561 ³⁶Ste-Marie, E., Grémillet, D., Fort, J., Patterson, A., Brisson-Curadeau, É., Clairbaux, M., Perret, S.,
562 Speakman, J.R., Elliott, K.H. (2022) Accelerating animal energetics: high dive costs in a small
563 seabird disrupt the dynamic body acceleration – energy expenditure relationship. *J Exp Biol.* 225:
564 jeb243252. doi: 10.1242/jeb.243252.

565 ³⁷Fort, J., Robertson, G.J., Grémillet, D., Traisnel, G., Bustamante, P. (2014) Spatial Ecotoxicology:
566 Migratory Arctic Seabirds Are Exposed to Mercury Contamination While Overwintering in the
567 Northwest Atlantic. *Environ Sci Technol.* 48:11560–11567. doi:10.1021/es504045g.

568 ³⁸Jakubas, D., Wojczulanis, K. (2007) Predicting the sex of Dovekies by discriminant analysis.
569 *Waterbirds* 30:92–96. doi: 10.1675/1524-4695(2007)030[0092:PTSODB]2.0.CO;2.

570 ³⁹Wojczulanis, K., Jakubas, D., Stempniewicz, L. (2022) The Little Auk Alle alle: an ecological indicator
571 of a changing Arctic and a model organism. *Polar Biol.* 45:163-176. doi:10.1007/s00300-021-
572 02981-7.

573 ⁴⁰Konarzewski, M., Taylor, J.R.E. (1989) The influence of weather conditions on growth of Little Auk
574 Alle alle chicks. *Ornis Scand.* 20:112. doi:10.2307/3676877.

575 ⁴¹Sakamoto, K.Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., Wanless, S. (2009) Can
576 Ethograms Be Automatically Generated Using Body Acceleration Data from Free-Ranging
577 Birds? *PloS ONE* 4: e5379. doi:10.1371/journal.pone.0005379.

578 ⁴²Patterson, A., Gilchrist, H.G., Chivers, L., Hatch, S., Elliott, K. (2019) A comparison of techniques for
579 classifying behavior from accelerometers for two species of seabird. *Ecol Evol.* 9:3030-3045. doi:
580 10.1002/ece3.4740.

581 ⁴³Wilson, R.P., Börger, L., Holton, M.D., Scantlebury, D.M., Gómez-Laich, A., Quintana, F., Rosell, F.,
582 Graf, P.M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Geraldi, N.R., Duarte, C.M., Scott,
583 R., Strano, M.S., Robotka, H., Eizaguirre, C., Fahlman, A., Shepard, E.L.C. (2020) Estimates for
584 energy expenditure in free-living animals using acceleration proxies: A reappraisal. *J Anim Ecol.*
585 89:161-172. doi:10.1111/1365-2656.13040.

586 ⁴⁴Wojczulanis-Jakubas, K., Waż, P., Jakubas, D. (2020) Little auks under the midnight sun: diel activity
587 rhythm of a small diving seabird during the Arctic summer. *Pol Res.*
588 doi:10.33265/polar.v39.3309.

589 ⁴⁵Welcker, J., Harding, A.M.A., Karnovsky, N.J., Steen, H., Strøm, H., Gabrielsen, G.W. (2009)
590 Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *J Avian*
591 *Biol.* 40: 388–399. doi:10.1111/j.1600-048X.2008.04620.x.

592 ⁴⁶Brown, Z.W., Welcker, J., Harding, A.M.A., Walkusz, W., Karnovsky, N. (2012) Divergent diving
593 behaviour during short and long trips of a bimodal forager, the little auk (*Alle alle*). *J Avian Biol.*
594 43:215-226. doi: 10.1111/j.1600-048X.2012.05484.x.

595 ⁴⁷Jakubas, D., Wojczulanis-Jakubas, K., Iliszko, L., Darecki, M., Stempniewicz, L. (2014) Foraging
596 strategy of the little auk *Alle alle* throughout breeding season –switch from unimodal to bimodal
597 pattern. *J Avian Biol.* 45:551-560. doi: 10.1111/jav.00303.

598 ⁴⁸Luque, S.P. (2007) Diving Behaviour Analysis in R. *R News* 7: 8-14.

599 ⁴⁹Elliot, K.H., Davoren, G., Gaston, A.J. (2008) Time allocation by a deep-diving bird reflects prey type
600 and energy gain. *Anim Behav.* 75: 1301-1310. doi:10.1016/j.anbehav.2007.09.024.

601 ⁵⁰Bustamante, P., Lahaye, V., Durnez, C., Churlaud, C., Caurant, F. (2006) Total and organic Hg
602 concentrations in cephalopods from the North Eastern Atlantic waters: Influence of geographical
603 origin and feeding ecology. *Sci Tot Environ.* 368: 585–596. doi:10.1016/j.scitotenv.2006.01.038.

604 ⁵¹Evers, D.C., Burgess, N.M., Champoux, L., Hoskins, B., Major, A., Goodale, W.M., Taylor, R.J.,
605 Poppenga, R., Daigle, T. (2005) Patterns and interpretation of mercury exposure in freshwater
606 avian communities in northeastern north America. *Ecotoxicology* 14:193–221.
607 doi:10.1007/s10646-004-6269-7.

608 ⁵²Chastel, O., Fort, J., Ackerman, J.T., Albert, C., Angelier, F., Basu, N., Blévin, P., Brault-Favrou, M.,
609 Bustnes, J.O., Bustamante, P., Danielsen, J., Descamps, S., Dietz, R., Erikstad, K.E., Eulaers, I.,
610 Ezhov, A., Fleishman, A.B., Gabrielsen, G.W., Gavrilov, M., Gilchrist, G., Gilg, O., Gíslason, S.,
611 Golubova, E., Goutte, A., Grémillet, D., Hallgrímsson, G.T., Hansen, E.S., Hanssen, S.A., Hatch,
612 S., Huffeldt, N.P., Jakubas, D., Jónsson, J.E., Kitaysky, A.S., Kolbeinsson, Y., Krasnov, Y.,
613 Letcher, R.J., Linnebjerg, J.F., Mallory, M., Merkel, F.R., Moe, B., Montevecchi, W.J., Mosbech,
614 A., Olsen, B., Orben, R.A., Provencher, J.F., Ragnarsdóttir, S.B., Reiertsen, T.K., Rojek, N.,
615 Romano, M., Søndergaard, J., Strøm, H., Takahashi, A., Tartu, S., Thórarinnsson, T.L., Thiebot,
616 J.B., Will, A.P., Wilson, S., Wojczulanis-Jakubas, K., Yannic, G. (2022) Mercury contamination
617 and potential health risks to Arctic seabirds and shorebirds. *Sci Total Environ.* 844: 156944. doi:
618 10.1016/j.scitotenv.2022.156944.

619 ⁵³Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., Peterson, S.H., Evers, D.C.,
620 Jackson, A.K., Elliot, J.E., Vander Pol, S.S., Bryan, C.E. (2016) Avian mercury exposure and
621 toxicological risk across western North America: A synthesis. *Sci Total Environ.* 568:749-769.
622 doi:10.1016/j.scitotenv.2016.03.071.

623 ⁵⁴Karnovsky, N., Harding, A., Walkusz, W., Kwaśniewski, S., Goszczko, I., Wiktor, J., Routti, H., Bailey,
624 A., McFadden, L., Brown, Z., Beaugrand, G., Grémillet, D. (2010) Foraging distributions of little
625 auks *Alle alle* across the Greenland Sea: implications of present and future Arctic climate change.
626 *Mar Ecol Prog Ser.* 415: 283–293. doi:10.3354/meps08749.

627 ⁵⁵Amélineau, F., Grémillet, D., Bonnet, D., Le Bot, T., Fort, J. (2016) Where to Forage in the Absence of
628 Sea Ice? Bathymetry as a key factor for an Arctic seabird. *PLoS ONE* 11:e0157764. doi:10.1371/
629 journal.pone.0157764.

630 ⁵⁶Spreen, G., Kaleschke, L., Heygster, G. (2008) Sea ice remote sensing using AMSR-E 89-GHz
631 channels. *J Geophys Res.* 113: C02S03. doi:10.1029/2005JC003384.

632 ⁵⁷R Core Team (2021) R: A language and environment for statistical computing. R Foundation for
633 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

634 ⁵⁸Lenth, R. (2019) Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version
635 1.4.3.01. <https://CRAN.R-project.org/package=emmeans>.

636 ⁵⁹Bates, D., Maechler, M., Bolker, B., Walker, S. (2015) Fitting Linear Mixed-Effects Models Using
637 lme4. *J Stat Soft.* 67:1-48. doi:10.18637/jss.v067.i01.

638 ⁶⁰Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B. (2017) “lmerTest Package: Tests in Linear Mixed
639 Effects Models.” *J Stat Soft.* 82:1-26. doi:10.18637/jss.v082.i13.

640 ⁶¹Regular, P.M., Hedd, A., Montevecchi, W.A., Robertson, G.J., Storey, A.E., Walsh, C.J. (2014) Why
641 timing is everything: Energetic costs and reproductive consequences of resource mismatch for a
642 chick-rearing seabird. *Ecosphere* 5:1-13. doi:10.1890/ES14-00182.1.

643 ⁶²Su, Y., Yajima, M. (2021) R2jags: Using R to Run ‘JAGS’_. R package version 0.7-1,
644 <<https://CRAN.R-project.org/package=R2jags>>.

645 ⁶³Douma, J.C., Weedon, J.T. (2019) Analysing continuous proportions in ecology and evolution: A
646 practical introduction to beta and Dirichlet regression. *Methods Ecol Evol.* 10:1412-1430.
647 doi:10.1111/2041-210X.13234.

648 ⁶⁴Maier, M.J. (2021) DirichletReg: Dirichlet Regression. R package version 0.7-1.
649 <https://github.com/maiermarco/DirichletReg>.

650 ⁶⁵Lovvorn, J.R., Grebmeier, J.M., Cooper, L.W., Bump, J.K., Richman, S.E. (2009) Modeling marine
651 protected areas for threatened eiders in a climatically changing Bering Sea. *Ecol Appl.* 19:1596–
652 1613. doi:10.1890/08-1193.1.

653 ⁶⁶Siegel, J.M. (2009) Sleep viewed as a state of adaptive inactivity. *Nat Rev Neurosci.* 10:747–753.
654 doi:10.1038/nrn2697.

655 ⁶⁷Elliott, K.H., Le Vaillant, M., Kato, A., Gaston, A.J., Ropert-Coudert, Y., Hare, J.F., Speakman, J.R.,
656 Croll, D. (2014) Age-related variation in energy expenditure in a long-lived bird within the
657 envelope of an energy ceiling. *J Anim Ecol.* 83:136-46. doi:10.1111/1365-2656.12126.

658 ⁶⁸Wojczulanis, K., Jakubas, D., Stempniewicz, L. (2005) Changes in the Glaucous Gull predation pressure
659 on Little Auks in southwest Spitsbergen. *Waterbirds* 28:430-435.

660 ⁶⁹Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K.,
661 Wojczulanis-Jakubas, K. (2019) Parental Coordination of Chick Provisioning in a Planktivorous
662 Arctic Seabird Under Divergent Conditions on Foraging Grounds. *Front Ecol Evol.* 7:349.
663 doi:10.3389/fevo.2019.00349.

664 ⁷⁰Courbin, N., Chinho, T., Pichegru, L., Verma-Grémillet, A., Péron, C., Ryan, P.G., Grémillet, D. 2020.
665 The dance of the Cape gannet may contain social information on foraging behaviour. *Anim*
666 *Behav.* 166: 95-108. doi:10.1016/j.anbehav.2020.06.012.

667 ⁷¹Jakubas, D., Iliszko, L., Wojczulanis-Jakubas, K., Stempniewicz, L. (2012) Foraging by little auks in the
668 distant marginal sea ice zone during the chick-rearing period. *Polar Biol.* 35:73–81.
669 doi:10.1007/s00300-011-1034-x.

670 ⁷²Fayet, A.L., Clucas, G.V., Anker-Nilssen, T., Syposz, M., Hansen, E.S. (2021) Local prey shortages
671 drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *J Anim Ecol.*
672 90: 1152-1164. doi:10.1111/1365-2656.13442.

673 ⁷³Boersma, P.D., Rebstock, G.A. (2009) Foraging distance affects reproductive success in Magellanic
674 penguins. *Mar Ecol Prog Ser.* 375: 263–275. doi:10.3354/meps07753.

675 ⁷⁴Jakubas, D., Trudnowska, E., Wojczulanis-Jakubas, K., Iliszko, L., Kidawa, D., Darecki, M.,
676 Błachowiak-Samołyk, K., Stempniewicz, L. (2013) Foraging closer to the colony leads to faster
677 growth in little auks. *Mar Ecol Prog Ser.* 489: 263–278. doi:10.3354/meps10414.

678 ⁷⁵Kooyman, G.L., Ponganis, P.J. (1998) The physiological basis of diving to depth: birds and mammals.
679 *Annu Rev Physiol.* 60:19-32. doi:10.1146/annurev.physiol.60.1.19.

- 680 ⁷⁶Williams, C.L., Meir, J.U., Ponganis, P.J. (2011) What triggers the aerobic dive limit? Patterns of
681 muscle oxygen depletion during dives of emperor penguins. *J Exp Biol.* 214:1802-1812.
682 doi:10.1242/jeb.052233.
- 683 ⁷⁷Piscopo, M., Notariale, R., Tortora, F., Lettieri, G., Palumbo, G., Manna, C. (2020) Novel Insights into
684 Mercury Effects on Hemoglobin and Membrane Proteins in Human Erythrocytes. *Molecules*
685 25:3278. doi:10.3390/molecules25143278.
- 686 ⁷⁸Alazoumi, K.K.M., Ahmed, A., Alamery, S.F., Shamsi, A., Ahmad, B., Islam, A., Farooqi, H. (2021)
687 Effect of Antioxidants on Heavy Metals Induced Conformational Alteration of Cytochrome C and
688 Myoglobin. *Protein Pept Lett.* 28:31-42. doi:10.2174/0929866527666200610134442.
- 689 ⁷⁹Auer, S.K., Salin, K., Anderson, G.J., Metcalfe, N.B. (2015) Aerobic scope explains individual variation
690 in feeding capacity. *Biol Lett.* 11:20150793. doi:10.1098/rsbl.2015.0793.
- 691 ⁸⁰Enstipp, M.R., Bost, C-A., Le Bohec, C., Bost, C., Laesser, R., Le Maho, Y., Bost, C., Laesser, R., Le
692 Maho, Y., Weimerskirch, H., Handrich, Y. (2019) The dive performance of immature king
693 penguins following their annual molt suggests physiological constraints. *J Exp Biol.*
694 222:jeb208900. doi:10.1242/jeb.208900.
- 695 ⁸¹Grunst, A.S., Grunst, M.L., Grémillet, D., Kato, A., Bustamante, P., Albert, C., Brisson-Curadeau, É.,
696 Clairbaux, M., Cruz-Flores, M., Gentès, S., Perret, S., Ste-Marie, E., Wojczulanis-Jakubas, K.,
697 Fort, J. (2022) Data for: Mercury contamination challenges the behavioural response of a
698 keystone species to Arctic climate change. Zenodo: doi:10.5281/zenodo.7185806, Dryad:
699 doi:10.5061/dryad.dbrv15f4t.

700