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

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

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

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

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

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

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

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

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

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

Methods

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

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

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

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

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

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

We also used accelerometer data to determine durations of foraging trips, dives, inter-dive intervals, and flights, proportion time spent flying during foraging trips versus around the colony (hereafter, proportion foraging flight), and chick provisioning rates. Breeding little auks display a dual foraging strategy, with short trips used for provisioning chicks and longer trips for self-maintenance. We assumed that short and long trips derive from two log-normal distributions⁴⁵. We log-transformed trip duration, and used K-mean clustering in R (R Core 2021) to group foraging trips into two categories. The cutoff value separating short and long trips was 3.9 hrs., which is lower than previously published values (~5.5-6 hrs.)^{46,47}. However, we preferred to use the value deriving from our dataset. We determined whether time on the water surface was part of a dive bout (inter-dive interval) using the standard classification method in R package diveMove⁴⁸. The bout ending criteria was 308 sec, and we assumed dives were ≤ 120 sec³⁶.

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

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

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

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

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

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

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

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

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

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

Results

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

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

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

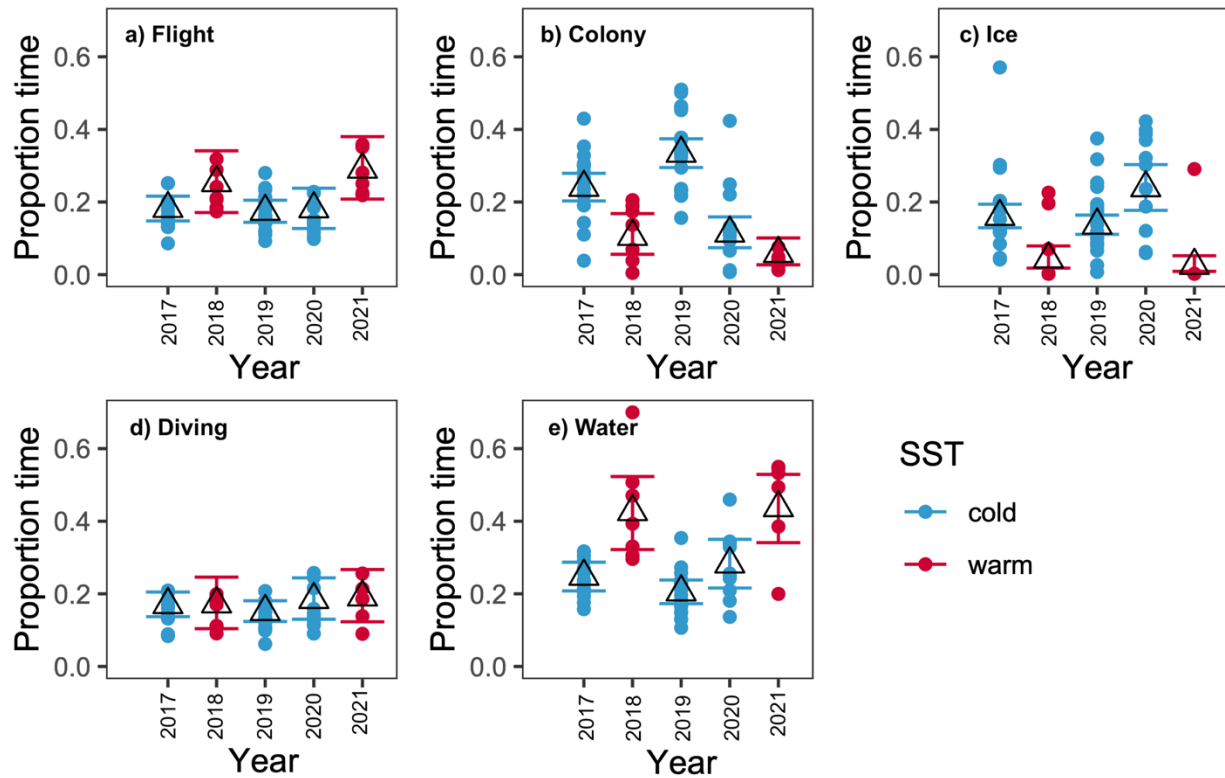


Figure 1. Little auk TABs across years at Ukaleqarteq, East Greenland. Relatively cold (blue; average SST < 2.5°C) and warm (red; average SST > 3.5°C) SST years are differentiated by color to facilitate visualization of differences in behavior associated with warmer conditions. Open triangles are predicted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

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

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

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

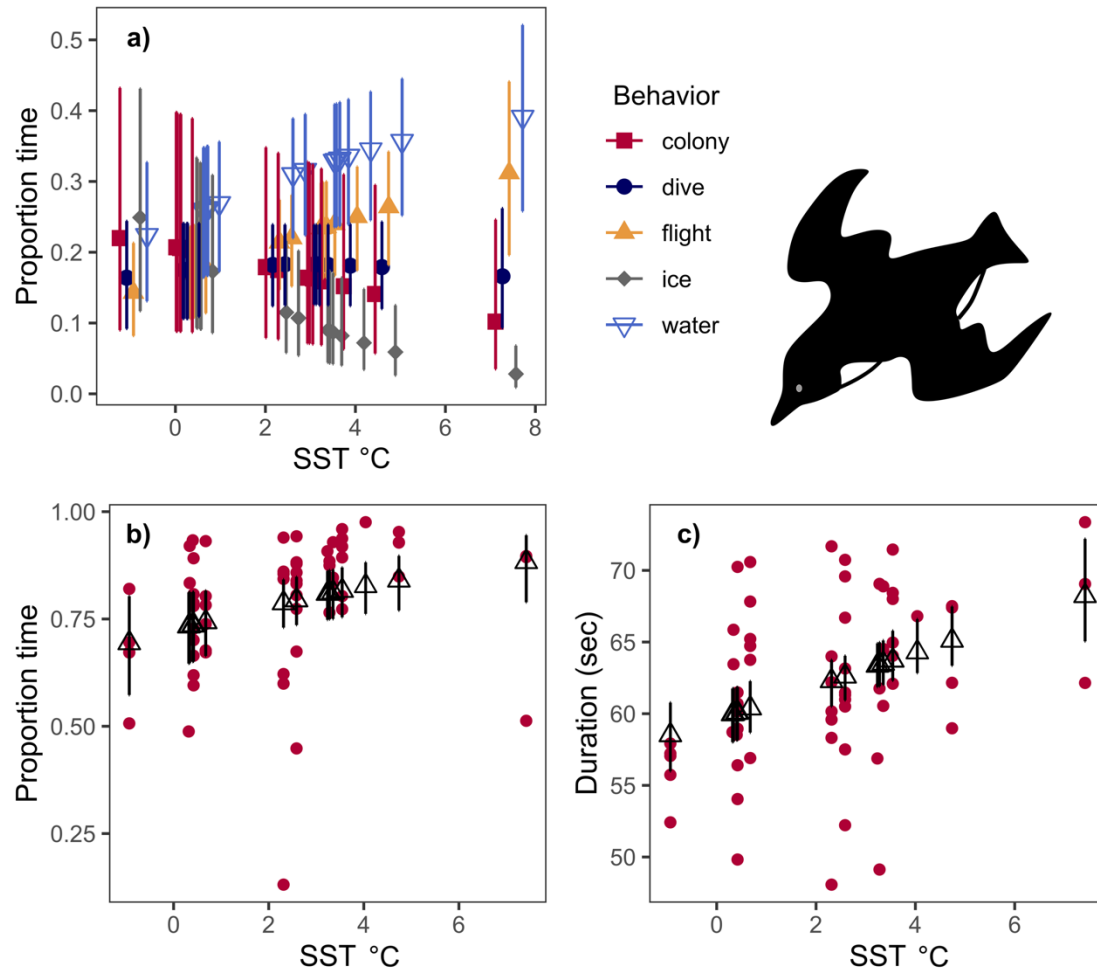


Figure 2. Little auk a) TABs (points staggered to facilitate viewing), b) proportion time deep versus shallow diving, and c) deep dive duration at Ukaleqarteq, East Greenland, as a function of increasing SST, with year as a random effect. Shapes at the center of error bars are predicted means, and error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

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

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

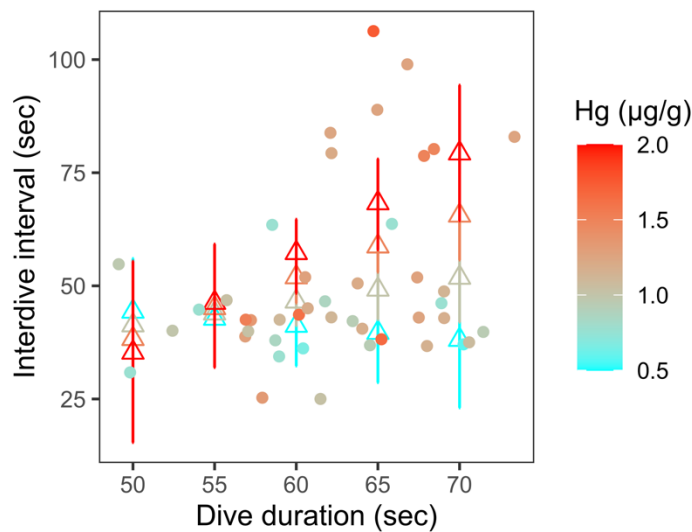


Figure 3. Interaction between dive duration and Hg concentrations in predicting inter-dive durations between deep dives for little auks at Ukaleqarteq. Open triangles are predicted values with 95% CIs for birds with Hg concentrations spanning the observed range. Closed points are observed values. Birds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

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

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

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

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

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

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

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

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

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

Supporting Information: Additional statistical results, which were too extensive to include in the main text.

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