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ARTICLE

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A keystone avian predator faces elevated energy expenditure in a warming Arctic

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Abstract

Climate change is transforming bioenergetic landscapes, challenging behavioral and physiological coping mechanisms. A critical question involves whether animals can adjust behavioral patterns and energy expenditure to stabilize fitness given reconfiguration of resource bases, or whether limits to plasticity ultimately compromise energy balance. In the Arctic, rapidly warming temperatures are transforming food webs, making Arctic organisms strong models for understanding biological implications of climate change-related environmental variability. We examined plasticity in the daily energy expenditure (DEE) of an Arctic seabird, the little auk (*Alle alle*) in response to variability in climate change-sensitive drivers of resource availability, sea surface temperature (SST) and sea ice coverage (SIC), and tested the hypothesis that energetic ceilings and exposure to mercury, an important neurotoxin and endocrine disrupter in marine ecosystems, may limit scope for plasticity. To estimate DEE, we used accelerometer data obtained across years from two colonies exposed to distinct environmental conditions (Ukaleqarteq [UK], East Greenland; Hornsund [HS], Svalbard). We proceeded to model future

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changes in SST to predict energetic impacts. At UK, high flight costs linked to low SIC and high SST drove DEE from below to above 4 × basal metabolic rate (BMR), a proposed energetic threshold for breeding birds. However, DEE remained below 7 × BMR, an alternative threshold, and did not plateau. Birds at HS experienced higher, relatively invariable SST, and operated above 4 × BMR. Mercury exposure was unrelated to DEE, and fitness remained stable. Thus, plasticity in DEE currently buffers fitness, providing resiliency against climate change. Nevertheless, modeling suggests that continued warming of SST may promote accelerating increases in DEE, which may become unsustainable.

KEYWORDS
activity budgets, climate change, daily energy expenditure, dovekie, ecotoxicology, mercury, plasticity, sea surface temperature

INTRODUCTION

Climate change is reconfiguring bioenergetic landscapes by modifying trophic networks, redistributing resources (Bartley et al., 2019), and introducing energetic challenges, such as thermal stress (Sherwood & Huber, 2010) and disease (Zamora-Vilchis et al., 2012). These effects are manifest globally, but are especially pronounced in the Arctic, which is warming nearly four times faster than other regions, reducing summer sea ice coverage (SIC) and increasing sea surface temperature (SST) in the Arctic ocean (IPCC, 2021). These abiotic effects have energetic effects that cascade through food webs from the level of primary producers to top consumers (Eamer et al., 2013; Gilg et al., 2012; Post et al., 2013).

When forecasting effects of climate change, a critical question involves the capacity of animals to adjust activity budgets and daily energy expenditure (DEE) to stabilize fitness. Resource intake may be maintained by increasing foraging time (Harding et al., 2007), ranging farther to reach profitable foraging grounds (Grémillet et al., 2012; Kwasniewski et al., 2010), and shifting breeding times to track resource peaks (Regular et al., 2014). However, such plasticity might be limited by energetic ceilings that cannot be surpassed, at least without costs (Harding et al., 2009; Tinbergen & Verhulst, 2000). Across avian species, DEE during chick rearing clusters around ~4 × basal metabolic rate (BMR), suggesting energetic constraint (Drent & Daan, 1980), and an ultimate energetic ceiling of ~7 × BMR has been proposed for DEE in endotherms (Elliott et al., 2014; Hammond & Diamond, 1997). Moreover, different species adopt distinct strategies when adjusting energy expenditure (EE) to environmental challenges (Mueller & Diamond, 2001; Speakman et al., 2003; Wojczulanis-Jakubas, 2021). Some exhibit relatively fixed EE (Elliott et al., 2014; Tinbergen & Verhulst, 2000), dictated by intrinsic constraints (Drent & Daan, 1980; Halsey et al., 2019; Hammond & Diamond, 1997), with limited plasticity. Others appear resource limited, with EE increasing in response to improved resource supply (enabling hypothesis; Jodice et al., 2006; Speakman et al., 2003). On the other hand, others increase DEE with environmental challenges, such as resource shortage, which may stabilize energy intake (forcing hypothesis; Speakman et al., 2003; Welcker et al., 2009).

Scope for plasticity in EE may also be sensitive to individual state variables, including changes in bioenergetic traits due to chemical contaminate exposure (Amélineau et al., 2019; Elliott et al., 2014). For instance, the neurotoxin and endocrine disruptor mercury (Hg) affects energetic traits, such as metabolic scope and BMR (Chastel et al., 2022; Gerson et al., 2019; Gilmour et al., 2019). Mercury from anthropogenic emissions reaches remote regions via long-range transport and bioaccumulates up food chains (Jonsson et al., 2022). The methylated form is particularly hazardous for marine organisms (Chastel et al., 2022). Climate change is affecting dynamics of contaminant exposure, for example, by releasing Hg from permafrost (Krabbenhoft & Sunderland, 2013; Stern et al., 2012), deeming understanding interactive effects of climate change and contaminants on bioenergetics an urgent priority (AMAP, 2021).

We examined changes in DEE with climate change-sensitive environmental conditions in an Artic seabird, the little auk (or dovekie, *Alle alle*), by using bird-borne accelerometers to quantify DEE across 5 years at two breeding colonies. Declining summer SIC and warming SST is driving declines in energy-rich, cold water copepods, comprising the little auk's resource base (Kwasniewski et al., 2010), and altering activity patterns (Amélineau et al., 2019; Jakubas et al., 2017). We assessed the hypothesis that DEE increases with challenging foraging conditions (high SST, low SIC), but may be limited at some point (e.g., ~4 or 7 × BMR). We also projected trends in SST into the future and assessed energetic implications, evaluated evidence that Hg contamination constrains DEE, and tested for fitness effects. Our study grants insights into the extent to which flexible energy budgeting may stabilize fitness under climate change scenarios that are widely applicable across taxonomic groups and ecosystem types.

MATERIALS AND METHODS

Study sites

We studied little auk populations located in East Greenland (Ukaleqarteq (UK; Kap Høegh); 70°44′ N, 21°35′ W), and southwestern Spitsbergen (Hornsund (HS); 77°00′ N, 15°33′ E; Svalbard archipelago). The East Greenland Current transports cold, Arctic waters past UK (Hovinen et al., 2014). SST in the HS area is influenced by the West Spitsbergen Current, transporting warm Atlantic waters, and Sørkapp current, carrying cold water masses (Loeng, 1991). HS experiences warmer SST and less SIC than UK. At both sites, seasonal and annual variation in SST affects cold water-associated copepod availability, with the influence of cold and warm water masses changing annually at HS, and SIC further modifying foraging conditions at UK (Amélineau et al., 2019; Kwasniewski et al., 2010; Strzelewicz et al., 2022). Field work was authorized by the Greenland government (Ministry of Hunting, Fishing and Agriculture), Governor of Svalbard (20/00373-8, 20/00373-2) and Norwegian Animal Research Authority (20/230613).

Estimating SST and SIC

For both sites, we determined SST within the primary foraging ranges of little auks, as determined by GPS tracking (Amélineau et al., 2016; Jakubas et al., 2020; Karnovsky et al., 2003, 2010). The foraging range for UK was encompassed by −21.57° longitude on the west, −17.47° longitude on the east, 69.8° latitude on the south, and 71.65° latitude on the north (~160 × 200 km), and for HS by 13° longitude on the west, 16.28° longitude on the east, 76.1° latitude on the south, and 77.5° latitude on the north (~50 × 150 km). We extracted daily average SST and SIC (for UK only, due to absence of ice at HS) values within these foraging ranges from the National Oceanic and Atmospheric Administration's (NOAA's) interpolated SST (OISST) high resolution daily dataset (1/4° global grid; https://psl.noaa.gov/data/gridde/data.noaa.oisst.v2.highres.html), and the University of Bremen's Sea Ice Remote Sensing database (https://seaice.uni-bremen.de/sea-ice-concentration/amsre-amsr2/), respectively. Data were averaged across the foraging range and each bird's accelerometer deployment period. Additionally, SST data was obtained from the incubation to late chick rearing period (~June 1 to August 15) between 1986 (year of first DEE measurement at HS by a past study) and 2021 to assess change over time and project future changes. At HS, we only used SST as a metric of environmental variability, since there was no substantial SIC. See Appendix S1: Section S1 for further details regarding processing SST and SIC data.

Calculating DEE

Birds were captured at nesting sites, equipped with triaxial accelerometers attached to ventral feathers with Tesa tape (Axy4, Technosmart, 25 × 10 × 5 mm, 3.0 g with tape, ~2% of mass), and recaptured in 3–11 days to retrieve devices. Data collection started when chicks were ~3–6 days old, and spanned 5 years (2017–2021; between 20 July and 5 August; $N = 17$, 7, 20, 11, 7) at UK and 2 years (2020–2021; between 13 and 28 July; $N = 10$ per year) at HS.

We analyzed accelerometer data (50 Hz) in Igor Pro 9.0 (WaveMetrics, Inc., Lake Oswego, OR, USA) and Ethnographer 2.05 (Sakamoto et al., 2009). We differentiated behaviors via a custom-written script, which used a k-clustering analysis and surface temperature data from the accelerometer. Behavior was classified as: flying, at the colony, on sea ice, diving and on the water surface (see Grunst et al., 2023 for details). TAB data are presented in Appendix S1: Table S1 and Figure S1 for HS and in Grunst et al. (2023) for UK.

Ste-Marie et al. (2022) derived an equation to estimate DEE from TABs by measuring DEE, using doubly labeled water (DLW; John, 1998; Lifson & McClintock, 1966), and TABs, via accelerometery in the UK population, yielding estimates of activity-specific energetic costs:

$$\begin{aligned}\mathrm{DEE} = {} & 9.52\ \mathrm{kJ\ day}^{-1}\,\mathrm{g}^{-1}\left(\%\mathrm{Time}_{\mathrm{fly+dive}}\right)\\ & + 0.97\ \mathrm{kJ\ day}^{-1}\,\mathrm{g}^{-1}\left(\%\mathrm{Time}_{\mathrm{other}}\right),\end{aligned} \tag{1}$$

where $\%\mathrm{Time}_{\mathrm{fly+dive}} = \%$time flying and diving, and $\%\mathrm{Time}_{\mathrm{other}} = \%$time in other activities. We used Equation (1) to estimate DEE, Equation (2), also from Ste-Marie et al. (2022), which divided flight and dive components of EE:

$$\begin{aligned}\mathrm{DEE} = {} & 8.45\ \mathrm{kJ\ day}^{-1}\,\mathrm{g}^{-1}\left(\%\mathrm{Time}_{\mathrm{fly}}\right)\\ & + 10.93\ \mathrm{kJ\ day}^{-1}\,\mathrm{g}^{-1}\left(\%\mathrm{Time}_{\mathrm{dive}}\right)\\ & + 0.86\ \mathrm{kJ\ day}^{-1}\,\mathrm{g}^{-1}\left(\%\mathrm{Time}_{\mathrm{other}}\right),\end{aligned} \tag{2}$$

to assess which components of DEE were related to predictor variables.

DEE and SST using historical data

We compiled 12 site-year observations of average DEE of breeding little auks using data from Gabrielsen et al. (1991) ($n = 13$), Grémillet et al. (2012) ($n = 70$) and the present study. This dataset spanned 35 years (1986–2021) and three sites (UK, HS, and Kongsfjorden, KF). KF is another little auk colony in Svalbard, which experiences even warmer SST than HS due to influence of the West Spitzbergen current (Cottier et al., 2005).

Hypothetical energetic ceilings

We used the published BMR of little auks (177.9 KJ day^{-1}; ~1.087 KJ day^{-1} g^{-1} given an average mass of 163.7 g; Gabrielsen et al., 1991) to estimate 4 × BMR, which we used as a hypothetical energetic ceiling due to its historical use (Drent & Daan, 1980). We also calculated 7 × BMR, which has been proposed as an ultimate energetic limit for endotherms (Elliott et al., 2014). We assessed whether DEE plateaus at these, or another, level.

Mercury contamination

We collected ~0.2 mL of blood from the brachial vein. Blood was centrifuged 10 min at 3500 rpm to separated red blood cells (RBCs) from plasma. RBCs were stored in 70% ethanol, and freeze-dried for 48 h and homogenized before analyses. We measured total Hg in desiccated RBCs using an advanced Hg analyzer spectrophotometer (Altec AMA 254) at the Institute Littoral Environnement et Sociétés, La Rochelle University (Bustamante et al., 2006). We took two or three measurements of Hg concentration per sample, until the standard deviation was <10%. We measured a certified reference material (CRM; Lobster Hepatopancreas Tort-3; NRC, Canada; $[\text{Hg}] = 0.292 \pm 0.022$ μg g^{-1} dry weight [dw]) and performed blanks before each analysis session. The limit of detection for Hg and mean ± SD of Tort-3 measurements were 0.005 μg g^{-1} dw and 0.306 ± 0.004 μg g^{-1} dw, respectively.

Fitness-related traits

We measured morphometrics upon recapturing birds. As a condition metric, we calculated the scaled mass index (SMI; Peig & Green, 2009) for the populations separately, as HS birds are heavier (Wojczulanis-Jakubas et al., 2011). We used tarsus length to calculate SMI for UK birds, and flatten wing length for HS birds. These size metrics presented the highest mass-size correlations (UK: $r = 0.28$, $p = 0.038$; HS: $r = 0.39$, $p = 0.097$), and correlations for the other metric were low ($r = 0.08$ for UK wing; $r = -0.04$ for HS tarsus length).

We estimated nestling provisioning trips day^{-1} from accelerometer data, by tabulating colony visits lasting >30 s following a foraging trip of ≥5 dives. Video-recordings confirmed that such visits were consistently associated with provisioning. Food delivery rate to offspring is associated with chick growth rates and/or reproductive success in many seabird species (Pinaud et al., 2005; Suryan et al., 2002). We were unable to measure fledging success due to logistical difficulties that prevented sampling sufficiently late in the season (Amélineau et al., 2019).

Statistical analysis

We performed statistical analyses in R 4.1.2 (R Core Team, 2021). First, we used a linear model (LM) with site-year as a fixed effect, and Tukey-adjusted pairwise comparisons to assess site-year differences in DEE (emmeans package; Lenth, 2019). We also used Pearson correlations (*Hmisc* package; Harrell et al., 2019) to assess relationships between components of EE (i.e., DEE, EE while flying and diving) at the two sites. Second, we used linear mixed effect models with Satterthwaite approximations for degrees of freedom (LMMs; lme4 and lmerTest packages; Bates et al., 2015; Kuznetsova et al., 2017), DEE as a response variable and SST or SIC (UK only), and Hg as fixed effects to explore relationships between DEE, environmental variables and Hg levels at the two sites separately. The interaction between either SST or SIC (log transformed) and Hg was included as a fixed effect, and year as a random effect. To assess which components of EE might mediate differences in DEE, we repeated the analysis using the flight, dive, and "other" components of EE. Third, we used an LMM to test for a relationship between average DEE and SST across the 12 site-year observations of DEE compiled from our current data and the data of past studies, with SST as a fixed effect and site as a random effect. Fourth, to examine future effects on DEE, we assessed temporal trends in SST at both sites using generalized additive models (GAMs; package *mgcv*; Wood, 2017), to allow for non-linear relationships between year, date, and SST. We fit a model with daily average SST between June 1 and August 15 as the response variable, year and date as smoothed terms, a tensor product interaction (ti term) between year and date, and a covariance structure (coAR1) to account for temporal autocorrelation. We used this model to predict SST 36 years in the future. The year-by-date interaction was removed when non-significant. We used predicted values of SST from GAMs, and equations generated from our data predicting DEE from SST at UK, to explore the projected increase in average DEE and total EE during chick-rearing (~July 1–August 15) between 1986 and 2021 (36 years; between the first and last year with DEE observations), and 2021 and 2057 (next 36 years). We present values using the equation predicting DEE from SST using UK data. The equation derived from the 12 site-year observations yielded similar results. Finally, we used LMMs to explore relationships between fitness traits (SMI, chick feeding rate), DEE, SST, and Hg at the sites separately. We entered DEE, SST, Hg, and their two-way interactions as fixed effects and year as a random effect. We assessed multicollinearity in models using the vif function (car package; Fox & Weisberg, 2019). Variance inflation factors were <2 (Zuur et al., 2010). We standardized continuous predictor variables to facilitate interpretation of beta coefficients when including interactions in models (Schielzeth, 2010).

RESULTS

Variation in DEE with environmental conditions and Hg exposure

Environmental conditions (SST, SIC) varied among sites and years, with average SST ranging from below 0°C at UK in 2020, to 4.5°C at HS, to 5.9°C at UK in 2021. SIC at UK ranged from 0.02% to 14.8% (Appendix S1: Table S2). Little auk DEE was lower by 0.8 to 1.3 KJ g^{-1} day^{-1} at UK in years with cold SST and low SIC (2017, 2019, and 2020) as compared to at UK during the warmest year (2021), and during both years at HS ($F_{6,74} = 10.9$, $p < 0.001$; Figure 1a). For example, at UK in 2019, DEE (mean ± SE [95% CI]) was 3.58 ± 0.116 (3.35, 3.81) KJ day^{-1} g^{-1}, or 3.2 × BMR, compared to 4.90 ± 0.21 (4.48, 5.32) kJ day^{-1} g^{-1}, or 4.5 × BMR in 2021. At Hornsund, where SST was relatively warm, DEE was almost identical in the 2 years, at ~4.25 × BMR (Figure 1a; Appendix S1: Table S3 gives all site-year DEE values). Thus, little auk DEE exceeded 4 × BMR (4.35 KJ day^{-1} g^{-1}) under warm oceanic conditions, but remained below 7 × BMR (7.61 KJ day^{-1} g^{-1}) across sites and years.

Consistent with these results, in an LMM with year as a random effect, little auk DEE at UK was linearly, positively related to SST ($t_{14} = 4.99$, $p < 0.001$; Figure 1b), and negatively related to SIC ($t_{21} = -4.06$, $p < 0.001$; Figure 1c), with no evidence of plateauing. The full equations predicting DEE from SST and SIC deriving from UK data were: DEE = 3.48 (±0.15) + 0.21 (±0.04) KJ day^{-1} g^{-1} × (SST °C), and DEE = 3.13 (±0.25) − 0.17 (±0.04) KJ day^{-1} g^{-1} × log(SIC %). DEE was predicted to reach 4 and 7 × BMR at 4.19 and 19.9°C SST, and below 0.11 and 1.04e-9% SIC, respectively. The former SST occurs regularly at both sites, and average SST surpassed this level at UK in 2021, and both years at HS. The latter SST is outside the range experienced (Figure 1b). At HS, DEE was unrelated to SST, likely due to low variation in SST (Figure 1d).

Blood Hg concentrations were not predictive of DEE at either study site, independently or in interaction with SST/SIC (Appendix S1: Tables S4 and S5). Mean ± SE (95% CI) blood Hg was low at HS (0.461 ± 0.052 (0.357, 0.566) μg g^{-1}, range: 0.32–0.62 μg g^{-1}), deeming effects on DEE unlikely, but were higher at UK (1.088 ± 0.039 (1.01, 1.169) μg g^{-1}, range: 0.579–1.75 μg g^{-1}).

Components of DEE at UK and HS

Increases in DEE given warm SST and low SIC at UK were driven by high flight EE (SST: $\beta \pm SE = 0.36 \pm 0.06$, $t_{13} = 5.97$, $p < 0.001$; SIC: $\beta \pm SE = -0.37 \pm 0.09$, $t_{29} = -3.37$, $p < 0.001$). Diving EE was unrelated to SST ($\beta \pm SE = 0.06 \pm 0.07$, $t_{13} = 0.83$, $p = 0.421$) or SIC ($\beta \pm SE = 0.03 \pm 0.07$, $t_8 = 0.38$, $p = 0.716$), and flying EE ($r = 0.70$, $p < 0.001$, $n = 62$) and diving EE ($r = 0.68$, $p < 0.001$) positively correlated with DEE. At HS only diving EE positively correlated with DEE ($r = 0.86$, $p < 0.001$), and the correlation with flight EE was nonsignificant ($r = 0.04$, $p = 0.870$, $n = 20$). At UK, flight and dive EE were uncorrelated ($r = -0.05$, $p = 0.719$), while at HS flight and dive EE negatively correlated ($r = -0.47$, $p = 0.037$).

Little auk DEE and SST using historical data

Across 12 site-year observations deriving from three little auk populations, there was a non-significant positive relationship between SST and DEE ($\beta \pm SE = 0.16 \pm 0.09$, $t_{10} = 1.80$, marginal $R^2 = 0.23$, $p = 0.102$). However, removing a strong outlier from UK in 2006 resulted in a positive relationship between SST and DEE ($\beta \pm SE = 0.20 \pm 0.04$, $t_9 = 4.99$, marginal $R^2 = 0.71$, $p < 0.001$; Figure 2). The equation for DEE deriving from this model is: DEE = 3.63 (±0.15) + 0.20 (±0.04) KJ day^{-1} g^{-1} × (SST °C), such that DEE is predicted to surpass 4 and 7 × BMR at 3.56 and 19.8°C, respectively.

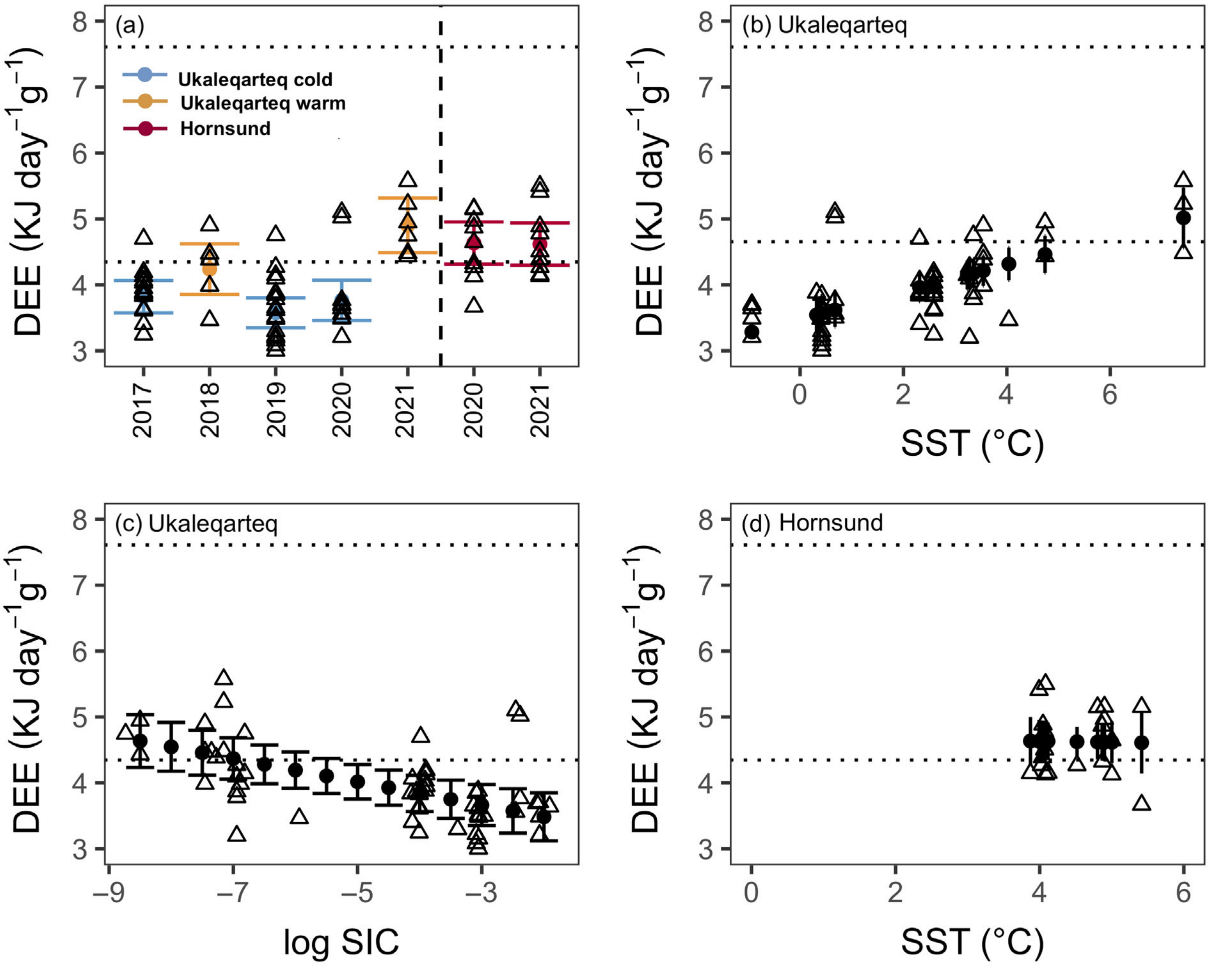

FIGURE 1 Variation in mass-specific DEE with (a) site-year, color coded with respect to average annual SST at UK (warm years >2.5°C; cold years <2.5°C), and with a distinct color for HS, (b) SST at UK, (c) SIC at UK and (d) SST at HS. Bars show 95% CIs around predicted values. Open triangles are observed values for individuals, with average SST/SIC and DEE calculated across accelerometer deployment periods. The vertical dashed line in (a) divides the sites. Dotted horizontal lines denote postulated DEE thresholds of ~4 and 7 × BMR. BMR, basal metabolic rate; DEE, daily energy expenditure; HS, Horsund; SIC, sea ice coverage; SST, sea surface temperature; UK, Ukaleqarteq.

Temporal SST trends and DEE

At both sites, SST increased between 1986 and 2021, and warmed seasonally with date. At UK, warming across years was date dependent, with rapid warming after ~July 10 (day 40; Figure 3a–c; Appendix S1: Table S6a). At HS, warming was not date dependent (Figure 3d–f; Appendix S1: Table S6b). If we predict average daily SST for 36 years after 2021 at UK, SST regularly exceeds 4°C (temperature at which predicted DEE exceeds 4 × BMR), by 23 July in 2057 (Figure 3c). Predicted SST never regularly exceeded 4°C during breeding at UK before 2016, when an SST of 4°C was not predicted until 14 August. At HS in 2057, predicted daily SST regularly exceeds 4°C by 1 June, the beginning of breeding (Figure 3f). However, SST sometimes crosses 4°C before these dates and before 2057, as in 2016 and 2021 at UK (Figure 3a), and as occurs regularly at HS (Figure 3d). The SST at which 7 × BMR is predicted to be exceeded (19.9°C) is not approached in the timeframe of our models.

At UK, average DEE during chick-rearing is predicted to increase to above 4 × BMR by 2057, from below this level in 1986 and 2021. At HS, average DEE during chick-rearing is predicted to increase from slightly above 4 × BMR in 1986 and 2021, to 4.5–4.6 × BMR by 2057. Furthermore, by 2057, total EE g^{-1}, summed across the chick rearing period, is predicted to increase by 15.5%–16.7% at UK, and by 10.7%–11.4% at HS, as compared to in 1986, with increases accelerating between 2021 and 2057 relative to between 1986 and 2021 (Table 1).

Fitness-related traits

SMI was unrelated to Hg level, DEE, SST, and interactions ($p > 0.10$; Appendix S1: Table S7). Chick feeding

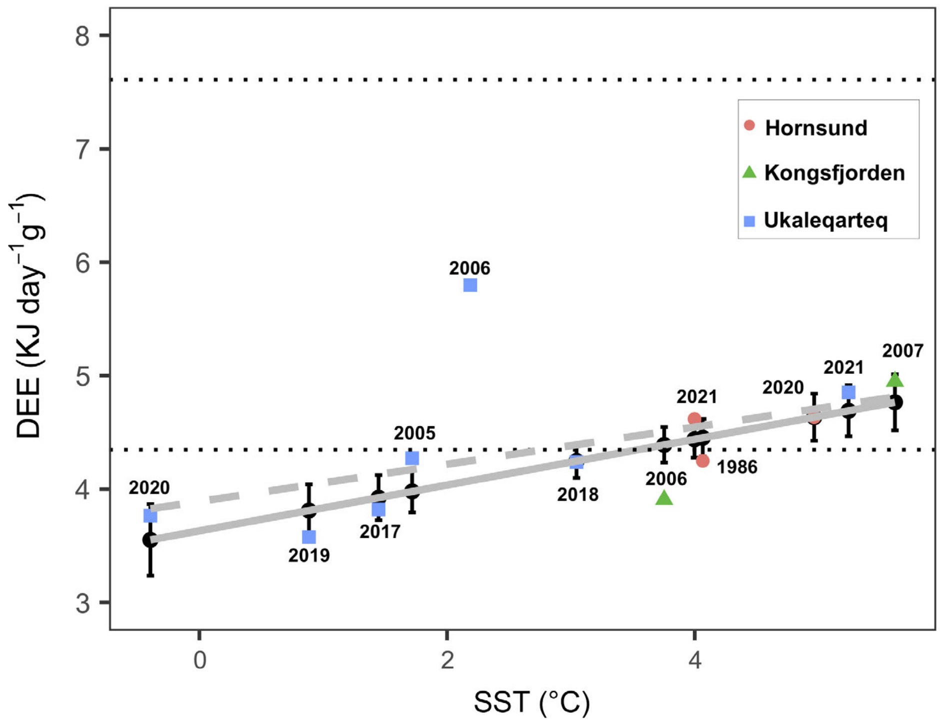

FIGURE 2 Relationship between average DEE of little auks and SST across 12 site-year observations from 1986 to 2021 at three sites. This relationship was non-significant when retaining the outlier (dashed line), but significant when removing this point (solid line). 95% CIs around predicted values are shown with the outlier removed. Points show experimental observations color-coded by study site. Observation year is indicated adjacent to each point. Dotted horizontal lines denote postulated DEE thresholds of ~4 and 7 × BMR. BMR, basal metabolic rate; DEE, daily energy expenditure; SST, sea surface temperature.

rate increased with DEE at UK ($\beta \pm SE = 0.42 \pm 0.15$, $t_{56} = 2.74$, $p = 0.008$), but not HS ($\beta \pm SE = 0.25 \pm 0.20$, $t_{18} = 1.26$, $p = 0.225$). At both study sites, SST, Hg and interactions were unrelated to provisioning rates ($p > 0.10$; Appendix S1: Table S8).

DISCUSSION

Energetic ceilings and co-exposure to multiple environmental stressors might limit organisms' capacity to adjust DEE, which could otherwise support population resiliency to climate change (Fossette et al., 2012; Von Bank et al., 2021). However, few studies have quantified scope for plasticity in DEE in response to climate change-associated stressors, even in the highly impacted Arctic. We demonstrate that DEE increases in a keystone Arctic seabird facing reduced cold water copepod abundance under warm oceanic conditions, with no evidence that an energetic threshold or Hg exposure is limiting plasticity. DEE in little auks at UK overshot the proposed energetic ceiling of 4 × BMR under conditions of warm SST and low SIC, whereas DEE at HS was slightly above 4 × BMR across the range in SST at this site, with DEE at both sites remaining well below 7 × BMR. However, modeling suggests continued increases in SST, which could magnify demands on DEE, threaten fitness and affect population dynamics.

Our study suggests that little auks flexibly manage energy use, increasing the capacity to maintain fitness with shifts in oceanic conditions and resource supply. Results from UK, and across little auk populations, are consistent with reduced resource supply elevating DEE (forcing hypothesis), as SST negatively correlates with availability of energy-rich prey (Carstensen et al., 2012). With increasing SST at UK, little auks flew farther to locate high quality resources to replenish body reserves and provision chicks, resulting in increased flight costs (Amélineau et al., 2019; Kwasniewski et al., 2010). In contrast, at HS, high DEE was associated with increased diving investment, indicating that adjustments in TABs differ between populations as a function of the environment. Parallel to our results, broad-billed hummingbirds (*Cynanthus latirostris*) flexibly managed energy use with changing resource availability, increasing DEE as floral resources became scarcer (Shankar et al., 2019). In contrast to our results, a past study on Kongsfjorden little auks found support for the enabling hypothesis, suggesting that tactics for flexibly managing

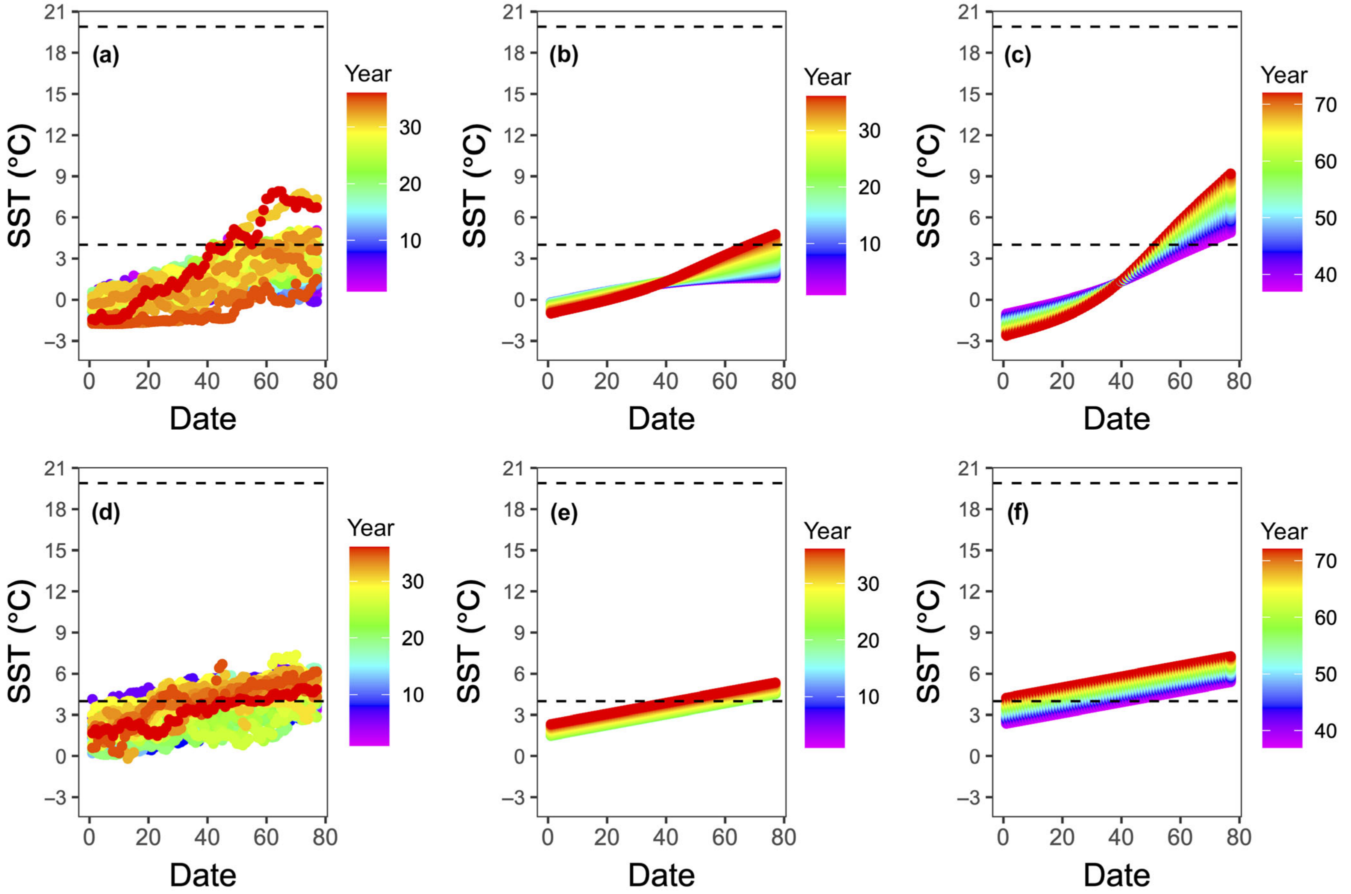

FIGURE 3 Temporal trends in sea surface temperature (SST) between June 1 (day 0) and August 15 (day 76), at Ukaleqarteq (UK) (a–c) and Horsund (HS) (d–f). Observed SST at (a) UK and (d) HS are shown between 1986 (Year 1) and 2021 (Year 36), along with predicted values from generalized additive models (GAMs) between 1986 and 2021 ([b] UK and [e] HS), and predicted values from GAMs projecting SST 36 years into the future, until 2057 (Year 72) ([c] UK [f] HS). The lower horizontal dashed line indicates 4°C, and the higher line 19.9°C, the temperatures at which daily energy expenditure is projected to surpass ~4 × BMR and ~7 × BMR.

TABLE 1 Predicted increases in average DEE during chick-rearing and total EE per gram across the chick-rearing period based on predicted increases in daily average SST at (a) UK and (b) HS.

			% increase (Total EE)	
	Average DEE (KJ day^{-1} g^{-1})	Total EE (KJ g^{-1})	From 1986	From 2021
(a) UK				
1986	3.85, 3.5 × BMR	177.1		
2021	4.12, 3.8 × BMR	189.5	7	
2057	4.49, 4.1 × BMR	206.7	16.7	9
(b) HS				
1986	4.40, 4.04 × BMR	202.2		
2021	4.49, 4.13 × BMR	206.6	2.2	
2057	4.90, 4.50 × BMR	225.3	10.7	9

Abbreviations: BMR, basal metabolic rate; DEE, daily energy expenditure; EE, energy expenditure; HS, Horsund; SST, sea surface temperature; UK, Ukaleqarteq.

energy may be context-dependent even within species (Welcker et al., 2009).

The capacity to adjust DEE to bioenergetic challenges is predicted to increase resiliency to climate change-associated environmental variation. Indeed, we observed no current impact of SST or SIC on little auk provisioning rates or body condition. However, species operating within tighter energetic constraints, due to higher costs or more limited supply, might demonstrate less plasticity. Understanding energetic limits and tradeoffs across diverse species, within the context of changing environments and species-specific traits, should be a future research priority.

Although scope remains before little auks reach energetic limits, increases in SST over time at UK and HS show accelerating trends that are projected to further reduce resources, and increase DEE. Fitness costs may result from both increases in mean SST, and increases in the frequency of high SST. At UK, SST is increasing most rapidly after ~July 30, during late chick rearing. At HS, SST is increasing moderately irrespective of date. Little auks could adjust breeding time to match favorable SST. Indeed, egg laying at HS advanced between 1970 and 2008 with warming SST (Moe et al., 2009). However, advances may be constrained, for instance, by snow melt limiting access to nest sites (Jakubas et al., 2016). At HS, where SST is relatively high, even slight increases in SST could affect cold water copepods, elevating energetic challenges. Indeed, among little auks in west Spitsbergen, in flow of warm Atlantic water and the percentage of Atlantic prey items in the diet negatively correlate with adult body mass, and chick growth rate and survival (Descamps et al., 2022). How far DEE can increase remains unclear, as do potential costs, as our fitness metrics were not comprehensive. Birds may be unable to sustain high DEE across multiple seasons, and there may also be survival costs (Hovinen et al., 2014; Jodice et al., 2006). Concerningly, little auk breeding colonies in Iceland have gone extinct due to climate change and human exploitation, with periods of decline characterized by high SST (Jakubas et al., 2022). However, there is no updated population estimate for East Greenland. In the only estimate available, from 1987, the East Greenland population was estimated at ~7 million, and the UK colony at 140,000 pairs (Kampp et al., 1987). According to Keslinka et al. (2019), the little auk population in all of HS is estimated at 591,892 pairs, and the studied population at 5981 pairs. In both cases, numbers are large and it is difficult to deduce population trends.

A current concern is that contaminant exposure could compound climate change-associated energetic challenges, threatening species resiliency (AMAP, 2021; Jenssen, 2006). However, we found no evidence that Hg contamination is affecting little auk energetics. Mercury concentrations at HS (mean: $0.461\ \mu g\ g^{-1}$ dw, or $0.097\ \mu g\ g^{-1}$ ww; assuming 79% blood moisture content) fell below the proposed minimum effect level for avian blood ($<0.2\ \mu g\ g^{-1}$ ww) (Ackerman et al., 2016; Chastel et al., 2022). However, Hg levels at UK (mean: $1.122\ \mu g\ g^{-1}$ dw, or $0.236\ \mu g\ g^{-1}$ ww) fell within the low risk range for toxicological effects ($0.2–1.0\ \mu g\ g^{-1}$ ww ww). A past study at UK documented negative correlations between adult body condition, chick growth and Hg levels across 11 years (Amélineau et al., 2019). Given mixed results to date, the importance of Hg contamination in this system deserves further investigation.

Finally, our data are subject to some sources of uncertainty. First, equations did not incorporate effects of environmental variables on activity-specific costs. The correlation between DEE estimated from accelerometer data and measured through DLW is high ($R^2 = 0.77$), and energetic costs of flying and diving account for the majority of DEE (Ste-Marie et al., 2022). Nevertheless, future studies should explore how activity-specific and resting metabolic energy costs are modified by environmental conditions to further inform how DEE will shift with climate change (Tremblay et al., 2022). In addition, instrumented birds may expend extra energy due to added mass and increased drag (Elliott et al., 2007). Thus, we cannot exclude that relationships observed between SST and DEE might differ somewhat in unhandicapped birds.

CONCLUSIONS

We demonstrate that rising SST and loss of sea ice, critical drivers of resource availability in Arctic marine ecosystems, promote increases in DEE in a keystone seabird. Plasticity in TABs and DEE buffer fitness effects, birds are not currently limited by an energetic threshold, and Hg contamination is not constraining DEE. However, *in lieu* of further plasticity, or energy gains that offset costs, accelerating increases in SST and DEE may become unsustainable. Little auks serve as ecosystem engineers, transferring nutrients between marine and terrestrial domains (González-Bergonzoni et al., 2017; Stempniewicz et al., 2007). Thus, changes in population dynamics due to increasing DEE could cascade to affect ecosystems.

AUTHOR CONTRIBUTIONS

Melissa L. Grunst, Andrea S. Grunst, Jérôme Fort, Katarzyna Wojczulanis-Jakubas, and David Grémillet conceived of the idea. Melissa L. Grunst wrote the manuscript. Jérôme Fort and David Grémillet (UK), and Katarzyna Wojczulanis-Jakubas and Dariusz Jakubas (HS) led data collection. Paco Bustamante and Akiko Kato provided expertise for Hg and accelerometer analyses. Eric Ste-Marie contributed to calculation of DEE. Céline Albert, Émile Brisson-Curadeau, Manon Clairbaux, Marta Cruz-Flores, Sophie Gentès, Antoine Grissot, and Samuel Perret collected and managed data. All authors approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Grunst et al., 2022) are available in Zenodo via the community of European Commission Funded Research (OpenAIRE) at https://doi.org/10.5281/zenodo.7334556.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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