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Andrea S Grunst, Melissa L Grunst, David Grémillet, Olivier Chastel, Marta Cruz-flores, et al.. Environment-dependent relationships between corticosterone and energy expenditure during reproduction: Insights from seabirds in the context of climate change. *Functional Ecology*, In press, 10.1111/1365-2435.14630 . hal-04673018

HAL Id: hal-04673018

<https://hal.science/hal-04673018>







Submitted on 19 Aug 2024

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RESEARCH ARTICLE

Environment-dependent relationships between corticosterone and energy expenditure during reproduction: Insights from seabirds in the context of climate change

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Funding information

Institut Polaire Français Paul Emile Victor, Grant/Award Number: 388; Region Nouvelle Aquitaine; Agence Nationale de la Recherche, Grant/Award Number: ANR-16-CE34-0005 and ANR-20-CE34-0006; Horizon 2020 Framework Programme, Grant/Award Number: 101024166, 101025549 and 896866; Narodowe Centrum Badań i Rozwoju, Grant/Award Number: 2017/25/B/NZ8/01417

Handling Editor: Kris Crandell

Abstract

1. Alternative hypotheses have been proposed regarding how the hormone corticosterone (CORT) mediates energy expenditure during reproduction. Elevated baseline CORT (CORT_b) could support daily energy expenditure (DEE), promoting reproductive effort or downregulate costly behaviours in low quality individuals facing allostatic overload.
2. We investigated relationships between CORT_b, time activity budgets (TABs), DEE and diving behaviour across 2 years and colonies of little auk (*Alle alle*), an Arctic seabird in which elevating DEE may support reproduction in the face of climate change.
3. We also explored whether mercury (Hg) contamination might suppress DEE by affecting the hypothalamus-pituitary-adrenal (HPA) axis and CORT production.
4. Furthermore, we performed phylogenetically controlled analysis across breeding seabird species to build broader understanding of CORT-DEE relationships.
5. CORT_b positively correlated with little auk activity, DEE and dive duration during a cold year in East Greenland, when CORT_b was elevated in the population, but not during a warmer year, or at Svalbard. CORT_b did not predict chick provisioning nor did Hg suppress CORT_b.
6. Across breeding seabird species, CORT_b and DEE were uncorrelated. Rather, contrary to predictions, CORT_b was higher in species breeding at lower latitudes.

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7. Intraspecific results suggest environment-dependent relationships between $CORT_b$, behaviour and DEE, with implications for understanding $CORT_b$'s role in climate change resiliency.
8. Interspecific analyses suggest absence of correlational selection between $CORT_b$ and DEE during reproduction, and that DEE thresholds that induce changes in $CORT_b$ might differ between species.

KEYWORDS

accelerometry, CORT-adaptation hypothesis, corticosterone, energy expenditure, mercury, phylogenetic analysis, thermal challenge

1 | INTRODUCTION

Life-history theory predicts that long-lived species should adjust energy expenditure to balance reproductive gains against survivorship costs (Stearns, 1992). The hormone corticosterone's (CORT) role in mediating this trade-off has generated debate. Corticosterone is released via the hypothalamus-pituitary-adrenal (HPA) axis in response to energetic and ecological stressors, and is involved in metabolic and behavioural regulation of allostasis (Landys et al., 2006; Wingfield et al., 1998). Baseline ($CORT_b$) and acutely elevated CORT act via different receptors to initiate different responses, binding with high and low affinity mineralocorticoid and glucocorticoid receptors, respectively (Lattin et al., 2012). Evidence suggests that suppressed acute adrenocortical responses promote reproduction over survivorship, guarding against abandonment of reproductive attempts (Bókony et al., 2009). $CORT_b$'s role in mediating reproductive effort appears more complicated, with positive and negative relationships between $CORT_b$ and reproductive effort having been documented (Angelier et al., 2007; Bonier, Martin, et al., 2009a; Bonier, Moore, et al., 2009b).

Moderately elevated $CORT_b$ may support energy expenditure during demanding reproductive periods, as $CORT_b$ regulates energy intake and metabolism (Hau et al., 2010; Landys et al., 2006). Past studies have reported positive correlations between $CORT_b$, activity and energy expenditure (Bonier, Martin, et al., 2009a; Bonier, Moore, et al., 2009b). Moreover, implanting CORT increases foraging activity, which could support reproduction given resource shortage (Angelier et al., 2007; Crossin et al., 2012). For example, CORT-implanted female macaroni penguins (*Eudyptes chrysolophus*) upregulated foraging and diving, leading to increased mass in females and their chicks (Crossin et al., 2012). The CORT-adaptation hypothesis proposes that elevated $CORT_b$ promotes fitness by supporting energy expenditure (Bonier, Martin, et al., 2009a; Bonier, Moore, et al., 2009b).

On the other hand, when environmental challenges overwhelm allostasis, increased $CORT_b$ can initiate an emergency life-history stage, wherein energy is allocated away from reproduction towards self-maintenance (Wingfield et al., 1998). In this case, higher $CORT_b$ is expected to correlate with reduced reproductive effort (and energy expenditure during reproduction) and fitness, as documented

in numerous studies (e.g. Angelier et al., 2010). The CORT-fitness hypothesis suggests that $CORT_b$ negatively correlates with fitness, as individuals less able to cope with environment challenges display higher $CORT_b$ and invest less in reproductive behaviours (Angelier et al., 2010; Bonier, Martin, et al., 2009a; Bonier, Moore, et al., 2009b).

Multiple factors likely contribute to variation in relationships between $CORT_b$, activity budgets, reproductive effort and fitness. Among these, variation in environmental conditions may be particularly important (Mohring et al., 2023). The CORT-fitness hypothesis assumes that $CORT_b$ is elevated in lower quality individuals, which perceive a given environment as more challenging (Bonier, Martin, et al., 2009a; Bonier, Moore, et al., 2009b). However, $CORT_b$ might also reflect varying environmental (e.g. thermal; Jessop et al., 2016) and reproductive (clutch size; Mohring et al., 2023) challenges that individuals expose themselves to. Elevated $CORT_b$ might hence arise in high quality individuals that invest intensively in reproduction, consistent with the CORT-adaptation hypothesis. Challenging environments could enhance positive relationships between $CORT_b$, energy expenditure and reproduction via feedbacks between behaviour and the HPA axis. Namely, engaging in costly behaviours under challenging conditions could elevate $CORT_b$, enabling continuance of costly behaviours.

Given that $CORT_b$ may support reproductive behaviours, contaminants that interfere with the HPA axis might disrupt these behaviours. Mercury (Hg) is a potent neurotoxin, which has been negatively correlated with $CORT_b$ in Foster's tern (*Sterna forsteri*) chicks (Herring et al., 2012) and tree swallows (*Tachycineta bicolor*) (Franceschini et al., 2009), and also reported to suppress adrenocortical stress responses (Moore et al., 2014), or increase $CORT_b$ (Scheiber et al., 2018). Therefore, Hg could limit animals' capacity to reproduce in challenging environments via HPA dysregulation. However, studies have also reported null Hg-CORT relationships (Tartu et al., 2015).

We adopted a multifaceted approach to assess the hypothesis that $CORT_b$ might support energetically demanding behaviour during reproduction, which is expected to affect fitness. First, we studied breeding little auks (*Alle alle*) across two colonies and years. We explored how environmental variation might affect relationships between $CORT_b$, time activity budgets (TABs), daily

energy expenditure (DEE), diving and fitness-related traits, including body condition and chick provisioning. Importantly, little auks are facing mounting environmental challenges due to Arctic climate change. Lower sea ice coverage (SIC) and higher sea surface temperature (SST) reduce abundance of little auks' energy rich copepods prey (Amélineau et al., 2019). Such conditions are increasing with climate change, and have been associated with elevated $CORT_b$ (Welcker et al., 2009) and DEE in little auks (Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Perret, et al., 2023a; Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Grissot, et al., 2023b). Hence, capacity to upregulate $CORT_b$ and DEE to support reproduction could become increasingly important as climate change progresses. However, warming sea and air (T_a) temperatures could also ease thermoregulatory demands, offsetting costs of foraging challenges and lowering $CORT_b$ (Amélineau et al., 2019). Greenlandic little auks are also exhibiting changes in Hg contamination with climate change, with evidence for negative reproductive outcomes (Amélineau et al., 2019). Thus, we explored whether Hg contamination could interfere with $CORT$ production, limiting DEE and climate change resiliency.

Second, to explore whether interspecific differences in $CORT_b$ reflect differences in DEE during breeding, suggesting correlational selection, we compiled published data from breeding seabirds regarding $CORT_b$, estimated DEE via modelling, and explored their correlation using phylogenetically controlled analyses. We hypothesised that $CORT_b$ and DEE would positively correlate and $CORT_b$ would be higher in high latitude breeders, which exhibit higher DEE (Dunn et al., 2018).

2 | METHODS

2.1 | Study populations; weather data

During June–August (2020, 2021), we studied little auks at two colonies: Ukaleqarteq (70°44' N, 21°35' W), East Greenland and Hornsund (77°00' N, 15°33' E), Svalbard (Spitsbergen). Fieldwork was authorised 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). All procedures were conducted in compliance with the ABS/ASAB Guidelines for the Use of Animals in Research and Teaching.

The East Greenland Current transports Arctic waters past Ukaleqarteq, promoting favourable foraging conditions (Karnovsky et al., 2010), but sea surface temperature (SST) and SIC vary inter-annually, with climate change promoting warming (Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Grissot, et al., 2023b). Hornsund is exposed to Arctic waters from Sørkapp current and Atlantic waters from West Spitsbergen current. Currents varies interannually, affecting foraging conditions (Jakubas et al., 2020). Cold temperatures and storms

also cause thermoregulatory and energetic challenges, evidenced by reduced chick growth (Amélineau et al., 2019). Daily average air temperature (T_a) for Ukaleqarteq was derived from a HOBO H21-USB weather station, and for Hornsund from the Polish Polar Station (Institute of Geophysics, Polish Academy of Science). We determined SST and sea surface chlorophyll-a (CHLA; phytoplankton productivity index) within little auks' foraging ranges, determined by GPS-tracking (Amélineau et al., 2019; Jakubas et al., 2020; see [Supporting Information](#)).

2.2 | Accelerometer deployment; blood sampling

We equipped adult little auks with accelerometers (Axy4, Technosmart, 25×10×5 mm, 3.0g, <2% body mass) during mid-chick rearing (13 July–5 August) to quantify TABs and diving. Numbers of equipped individuals were 11 and 7 at Ukaleqarteq in 2020 and 2021, and 10 annually at Hornsund. Birds were captured using noose carpets or lassos (Ukaleqarteq) or in nests (Hornsund), and recaptured within 3–11 days. Data <24 h long (reflecting battery failure) were excluded from TAB and DEE analyses, as short-term data yield inaccurate TAB/DEE estimates, but were used to quantify diving traits. Exclusions included two datasets from Ukaleqarteq in 2020 and 1 from Ukaleqarteq in 2021. At capture and recapture, we obtained ~0.2 mL blood samples within 3 min. Data from birds without accelerometer data were used in analyses involving variation of corticosterone with site-year/mercury, but lacked behavioural data (Table 1 for sample sizes). We did not distinguish sexes. Male and female little auks are similar in size, parental behaviour (Wojczulanis-Jakubas et al., 2022), and $CORT_b$ during incubation and chick rearing (Wojczulanis-Jakubas et al., 2013).

2.3 | Analysing accelerometer data and estimating DEE

We used Igor Pro 9.0 (WaveMetrics, Lake Oswego, OR, USA) to determine TABs (flying, diving, colony, ice, water) and behaviour (dive, inter-dive lengths) from accelerometry data. We subdivided dives into deep (descent >5s) and shallower dives (descent ≤5s) (Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Perret, et al., 2023a). We estimated DEE from TABs using activity-specific metabolic costs plus adjustments for thermoregulatory costs (see Supplement).

2.4 | Body condition; chick provisioning

We measured morphometrics upon recapturing birds. To assess condition, we calculated scaled mass index (SMI; Peig & Green, 2009) for the populations separately, as Hornsund little auks are larger (Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Grissot,

TABLE 1 Study design for (a) little auk study across two sites (Ukaleqarteq, East Greenland, Hornsund, Svalbard) and years (2020, 2021), and (b) phylogenetically controlled analysis across species.

Scale of inference	Sample sizes for different variables	Scale at which predictive variables were investigated	Number of replicates at appropriate scale (site-years)
(a) Little auk study		Site-years	3/4 ^a
Traits/comparisons examined			
CORT _b among sites-years	120 observations (31, 22, 46, 21) ^b ; 80 individuals (17, 17, 36, 15) ^b		
CORT _b with Hg/SMI	74 observations (21, 11, 27, 15); 43 individuals (11, 6, 18, 12)		
Dive length with CORT _b	38 individuals (11, 7, 10, 10)		
TAB/DEE with CORT _b	35 individuals (9, 6, 10, 10)		
(b) Phylogenetic analysis			
Species	Table S1 lists data lines per species	Species	41 species (104 studies)

Abbreviations: CORT_b, baseline corticosterone; DEE, daily energy expenditure; Hg, mercury; SMI, scale mass index; TAB, time activity budget.

^aHornsund 2020/2021 was collapsed into one category for CORT-behaviour and CORT-DEE analyses, due to no difference in environmental conditions or CORT between years.

^bSample sizes for: Ukaleqarteq 2020, Ukaleqarteq 2021, Hornsund 2020, Hornsund 2021. At Hornsund, 5 birds had CORT measured in both years and 4 Hg, CORT and SMI in both years.

et al., 2023b). We estimated provisioning trips/day from accelerometer data by tabulating colony visits lasting >30s following foraging trips containing ≥5 dives (Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Perret, et al., 2023a).

2.5 | Corticosterone (CORT) and mercury (Hg) analyses

We centrifuged blood (10 min, 3500rpm) to separate plasma from red blood cells (RBCs). Mercury was measured from samples taken at capture or recapture, and not expected to differ between time points. We measured CORT at both time points to estimate repeatability. RBCs were stored in 70% ethanol, freeze-dried for 48h and homogenised before Hg analyses. We froze plasma at -20°C in the field and later at -80°C.

We measured total Hg in RBCs using a Hg analyser spectrophotometer (Altec AMA 254) at the Institute Littoral Environnement et Sociétés, La Rochelle University (Bustamante et al., 2006). Two measurements were taken per sample (SD < 10%). We measured certified reference material (CRM; Lobster Hepatopancreas Tort-3; NRC, Canada; [Hg] = 0.292 ± 0.022 µg g⁻¹ dw) and performed blanks before sessions. Limit of detection (LOD) was 0.005 µg g⁻¹ dw and mean ± SD of Tort-3 measurements 0.306 ± 0.004 µg g⁻¹ dw. Plasma CORT was measured via radioimmunoassay at the Centre d'Etudes Biologiques de Chizé. We extracted CORT with diethyl-ether. Dried extract was re-dissolved in phosphate buffer and incubated overnight at 4°C with 3000 CPM of ³H-corticosterone (Perkin Elmer,

USA) and polyclonal rabbit antiserum (Sigma, USA). Bound and free fractions were separated via dextran-coated charcoal. After centrifugation, bound fraction activity was counted in a Tri-carb liquid scintillation counter 2810TR (Perkin Elmer, USA). Samples were measured in duplicate 50 µL aliquots in four assays. Intra-assay precision was 13.2%, inter-assay precision 17.0% and LOD 0.28 ng/mL.

2.6 | Baseline corticosterone (CORT_b) and DEE across species

Across seabirds, we assembled a dataset from the literature containing CORT and DEE measurements during incubation, early chick (brooding) and late chick (creche). Supplement contains search methodology and results.

DEE data that could be coupled with CORT data (same colony, stage) was scarce. Hence, we estimated DEE through a model derived from a phylogenetically controlled meta-analysis, available within a web-based app ('Seabird FMR Calculator', https://ruthe.dunn.shinyapps.io/seabird_fmr_calculator/; Dunn et al., 2018). This model estimates DEE (aka field metabolic rate or FMR) from body mass, latitude and reproductive stage. The model cannot estimate variation in DEE arising from year-to-year differences in weather or resources. Among-site variation is also not fully accounted for, although encompassed by latitude. Nonetheless, Pearson's correlation between observed and estimated mass-specific DEE was $r=0.957$, using data from 24 species with empirical DEE data. We compiled multiple data lines per species and colony, encompassing different years, sexes, and breeding stages.

Our analysis incorporated explanatory variables related to life history (longevity, clutch size; averages used when multiple measures available) and environmental conditions (T_a , SST, CHLA). We fit models using maximum longevity and clutch size to describe overall evolved potential in these characteristics, and using a current brood value index calculated as \log_{10} (average clutch size/(average clutch size * clutches per year * average lifespan)). Average lifespan was calculated via $1/(\text{adult annual mortality})$ (Bókony et al., 2009). [Supporting Information](#) contains the details.

2.7 | Replication statement

[Table 1](#) provides information regarding study design and sample sizes.

2.8 | Statistics

2.8.1 | Environmental conditions, mercury (Hg) and baseline corticosterone ($CORT_b$)

Analyses were performed in R 4.2.0 (R Core Team, 2022). To assess variation in environmental conditions (SST and T_a) and individual blood Hg among site-years, we used 3 separate ANOVAs with Tukey *post-hoc* tests. Phytoplankton productivity (CHLA) was not statistically compared between years, as only monthly averages were available. We used a linear mixed model (LMM, Gaussian family, identity link; packages *lmer4*, *lmerTest*; Bates et al., 2015; Kuznetsova et al., 2017) with Satterthwaite approximations to assess variation in $CORT_b$ (natural log-transformed; response) among site-years (fixed effect, 4 levels: Ukaleqarteq 2020, Ukaleqarteq 2021, Hornsund 2020, Hornsund 2021). Capture point (1–2) was included as a fixed effect and individual identity as a random effect. We did not include other covariates, because we were exploring how $CORT_b$ varied among site-years, rather than how other variables explained patterns. We used *rptR* (Stoffel et al., 2017) to assess repeatability of $CORT_b$ using variance components from this LMM, with a *p*-value from a loglikelihood test. We used *emmeans* to perform Tukey *post-hoc* comparisons (Lenth, 2022). Capture point was removed due to nonsignificance ($p > 0.15$), and as we did not expect $CORT_b$ to change across a narrow window of chick rearing. We performed an LMM with $CORT_b$ as response, average temperature (T_a) on capture day as a fixed effect, and site-year and individual as random effects to assess the T_a - $CORT_b$ relationship. We could not simultaneously enter T_a and site-year as fixed effects due to multicollinearity.

We performed another LMM to assess relationships between $CORT_b$ (response), Hg and SMI, because not all birds had Hg and SMI data, reducing sample size ($N = 74$ observations, 43 birds when including Hg/SMI; 120 observations, 80 birds when excluding them; [Table 1](#)). We included interactions between site-year, Hg and SMI as fixed effects and individual as a random effect.

2.8.2 | Baseline corticosterone ($CORT_b$), behaviour and DEE

We used beta regression (packages *betareg* and *mgcv*, Cribari-Neto & Zeileis, 2010; Wood et al., 2016) to model TAB, as reflected by proportion time in costly activities (flying/diving). We modelled DEE, dive duration, inter-dive duration and provisioning rate (four responses) using four linear models (LMs). We tested $CORT_b$ -by-site-year interactions to assess whether $CORT_b$ might correlate differently with DEE and behaviour within site-years with different environmental conditions. We collapsed the 2 years at Hornsund into one category, as they did not differ in environmental conditions, $CORT_b$ or Hg. We initially included interactions between $CORT_b$, Hg and SMI to assess whether effects of $CORT_b$ depended on these variables. We averaged $CORT_b$ across time points, as $CORT_b$ showed repeatability, with no significant change between sampling points.

Continuous predictors were standardised to mean zero, standard deviation one. We removed nonsignificant interactions ($p > 0.10$ in all cases) to assess main effects. We also removed nonsignificant SMI and Hg main effects ($p > 0.10$) to expand sample size (some birds lacked covariate data). Results from full and reduced models were similar ([Tables S2–S5](#)).

2.8.3 | Phylogenetically controlled analysis

To investigate the relationship between baseline corticosterone ($CORT_b$) and energy expenditure (DEE) across breeding seabird species, we used Bayesian phylogenetic linear mixed models (LMMs). We obtained 100 phylogenetic trees from [BirdTree.org](#) (Jetz et al., 2012; Hackett All Trees) and used package *multree* (Guillaume & Healy, 2014) to run *MCMCglmm* (Hadfield, 2010) across each tree, with parameter estimates and 95% credible intervals (CIs) averaged across models to account for phylogenetic uncertainty. We first predicted $CORT_b$ (log-transformed) from variables used to estimate DEE (latitude, breeding stage, mass), with sex, maximum longevity (log-transformed) and clutch size as life-history related predictors. In a second model, predictors were mass-specific DEE, sex, mass, environmental variables (SST, CHLA, T_a) and life-history variables. We averaged environmental variables across population-years, as DEE estimates could not be varied by year. Sea surface (SST) and air (T_a) temperatures were highly correlated ($r = 0.902$, $p < 0.001$). Thus, we ran this model two times to assess whether SST or T_a had a stronger effect but acknowledge that effects cannot be definitively disentangled. Random effects were species (phylogeny), population and year for model 1, and species and population for model 2. We used an uninformative inverse-Wishart prior distribution ($V = 0.5$, $\nu = 0.002$) and ran models for 50,000 iterations, with burn-in of 1000 and thinning of 100. We checked convergence via potential scale reduction factors (PSR), with $PSR < 1.1$, compared model fits using DIC and considered predictors significant if 95% CIs did not overlap zero.

3 | RESULTS

3.1 | Environmental conditions and baseline corticosterone (CORT_b)

At Ukaleqarteq, 2020 was colder (mean ± SE air temperature (T_a) = 4.737 ± 0.559, SST = 0.064 ± 0.113°C) and less productive (phytoplankton productivity (CHLA) = 0.331, 10.75% uncertainty) than 2021 (T_a = 8.972 ± 1.010°C, SST = 5.961 ± 0.351°C, CHLA = 0.597, 8.47% uncertainty). Daily average SST (°C) in little auks' foraging range was 1.6°C below, and 3.7°C above, a 35 year average in 2020 versus 2021. CHLA in July averaged 0.165 mg/m³ below, and 0.100 mg/m³ above, a 25 year average. At Hornsund, conditions were similar between years, with T_a and SST intermediate to Ukaleqarteq 2020 and 2021, and CHLA similar to Ukaleqarteq 2021 (Table S1). Blood Hg (µg g⁻¹ dw) was higher at Ukaleqarteq (mean ± SE = 1.185 ± 0.037) than Hornsund (0.479 ± 0.015; $t_{45,6}$ = -14.705, p < 0.001), but not different between years within sites (Table S1).

Baseline corticosterone (CORT_b) also differed among site-years ($F_{3,89}$ = 5.503, p = 0.002), being highest at Ukaleqarteq in 2020 (2.074 ± 0.447 ng/mL, N = 17) and lowest at Ukaleqarteq in 2021 (0.839 ± 0.199 ng/mL, N = 17). CORT_b at Hornsund was 1.985 ± 0.323 ng/mL in 2020 (N = 36) and 1.345 ± 0.327 ng/mL in 2021 (N = 15) (Table S2a). CORT_b was individually repeatable (r ± SE (95% CI) = 0.376 ± 0.133 (0.100, 0.639), p = 0.012) (Table S2a). After *post-hoc* Tukey tests, CORT_b differed between Ukaleqarteq in 2020 versus 2021, and Hornsund in 2020 versus Ukaleqarteq in 2021 (Table S2b). The model with site-year as a random effect and air temperature (T_a) as a fixed effect indicated that CORT_b increased with declining T_a (β ± SE = -0.322 ± 0.088, t_{126} = -3.655, p < 0.001). As T_a decreased from 15 to 1°C (range in dataset), CORT_b was predicted to increase from 0.705 to 2.352 ng/mL, by 1.647 ng/mL.

3.2 | Baseline corticosterone (CORT_b), mercury (Hg) and SMI

CORT_b was not related to blood Hg or SMI. We found nonsignificant interactions between site-year and Hg ($F_{3,34}$ = 0.859, p = 0.472) and SMI ($F_{3,57}$ = 1.381, p = 0.258; Table S3a). After removing interactions, main effects of Hg (β ± SE = 0.817 ± 0.460, t_{34} = 1.776, p = 0.085) and SMI (β ± SE = -0.081 ± 0.155, t_{34} = -0.523, p = 0.604) were nonsignificant (Table S3b).

3.3 | Baseline corticosterone (CORT_b) and TAB

Relationships between CORT_b and TAB depended on site-year (significant interaction; Table 2) but not mercury or SMI (nonsignificant interactions/main effects; Table S4). CORT_b positively correlated with flying/diving time within Ukaleqarteq 2020 (β ± SE = 0.256 ± 0.117, Z = 2.183, *Pseudo R*² = 0.329, p = 0.029) but not other site-years

TABLE 2 Beta regression for relationship between little auk baseline corticosterone (CORT_b) and proportion time flying/diving. Ukaleqarteq 2020 is the reference. Sample sizes: 9, 6 and 20 in Ukaleqarteq 2020, Ukaleqarteq 2021 and Hornsund (data from 2 years combined).

Variable	β ± SE	Z	p
Intercept	-0.736 ± 0.086	-8.590	<0.001
CORT _b	0.259 ± 0.096	2.698	0.007
Hornsund	0.447 ± 0.101	4.416	<0.001
Ukaleqarteq 2021	0.529 ± 0.140	3.781	<0.001
CORT _b × Hornsund	-0.283 ± 0.108	-2.620	0.009
CORT _b × Ukal. 2021	-0.390 ± 0.171	-2.282	0.022
<i>Pseudo R</i> ² = 0.479			
Phi (precision) = 69.93 ± 16.60, Z = 4.212, p < 0.001			

(Hornsund: β ± SE = -0.027 ± 0.053, Z = -0.512, *Pseudo R*² = 0.013, p = 0.609; Ukaleqarteq 2021: β ± SE = -0.100 ± 0.074, Z = -1.339, *Pseudo R*² = 0.311, p = 0.181). At Ukaleqarteq in 2020, predicted mean ± SE (95% CI) proportion time flying/diving was 0.273 ± 0.029 (0.215, 0.331) for birds with the lowest CORT_b (0.40 ng/mL) and 0.419 ± 0.043 (0.335, 0.504) for those with the highest (6.3 ng/mL) (Figure 1a), a difference of 14.6% (3.5 h/day). However, on average, little auks spent less time in costly behaviours within Ukaleqarteq 2020 [0.330 ± 0.021 (0.288, 0.372)] than 2021 [0.460 ± 0.027 (0.405, 0.515)] or at Hornsund [0.428 ± 0.015 (0.398, 0.457)] (Figure 1a).

At Ukaleqarteq in 2020, diving (β ± SE = 0.270 ± 0.127, Z = 2.127, *Pseudo R*² = 0.305, p = 0.033) changed more than flying (β ± SE = 0.128 ± 0.106, Z = 1.207, *Pseudo R*² = 0.115, p = 0.228) with CORT_b. Diving was predicted to increase from 0.126 ± 0.022 (0.082, 0.171) to 0.222 ± 0.039 (0.144, 0.300) between individuals with the lowest versus highest CORT_b (9.6%), and flying predicted to increase from 0.152 ± 0.021 (0.109, 0.195) to 0.199 ± 0.032 (0.136, 0.261) proportion time (4.7%).

3.4 | Baseline corticosterone (CORT_b) and DEE

Site-year and CORT_b interacted to predict DEE (Table 3). This was expected based on the analysis regarding relationships between CORT_b and TAB, as DEE is highly dependent on energetically demanding behaviour (note similarity between Figure 1a,b). CORT_b and DEE tended to positively correlate within Ukaleqarteq 2020 (β ± SE = 0.516 ± 0.250, t_7 = 2.065, p = 0.077, *R*² = 0.289), but not other site-years (Ukaleqarteq 2021: β ± SE = -0.096 ± 0.086, t_4 = 2.139, p = 0.331, *R*² = 0.042, Hornsund: β ± SE = -0.018 ± 0.036, t_{18} = -0.498, p = 0.625, *R*² = -0.041). For Ukaleqarteq 2020, birds with the lowest CORT (0.40 ng/mL) were predicted to expend a mean ± SE (95% CI) of 3.315 ± 0.280 (2.742, 3.888) kJ day⁻¹ g⁻¹, and those with the highest CORT (6.3 ng/mL) 4.351 ± 0.270 (3.797, 4.904) kJ day⁻¹ g⁻¹, a difference of 1.036 kJ day⁻¹ g⁻¹ (31.2%). However, DEE (kJ day⁻¹ g⁻¹) averaged lower at Ukaleqarteq in 2020 [3.85 ± 0.193 (3.46, 4.24)] than 2021 [4.77 ± 0.236 (4.29, 5.25)] and

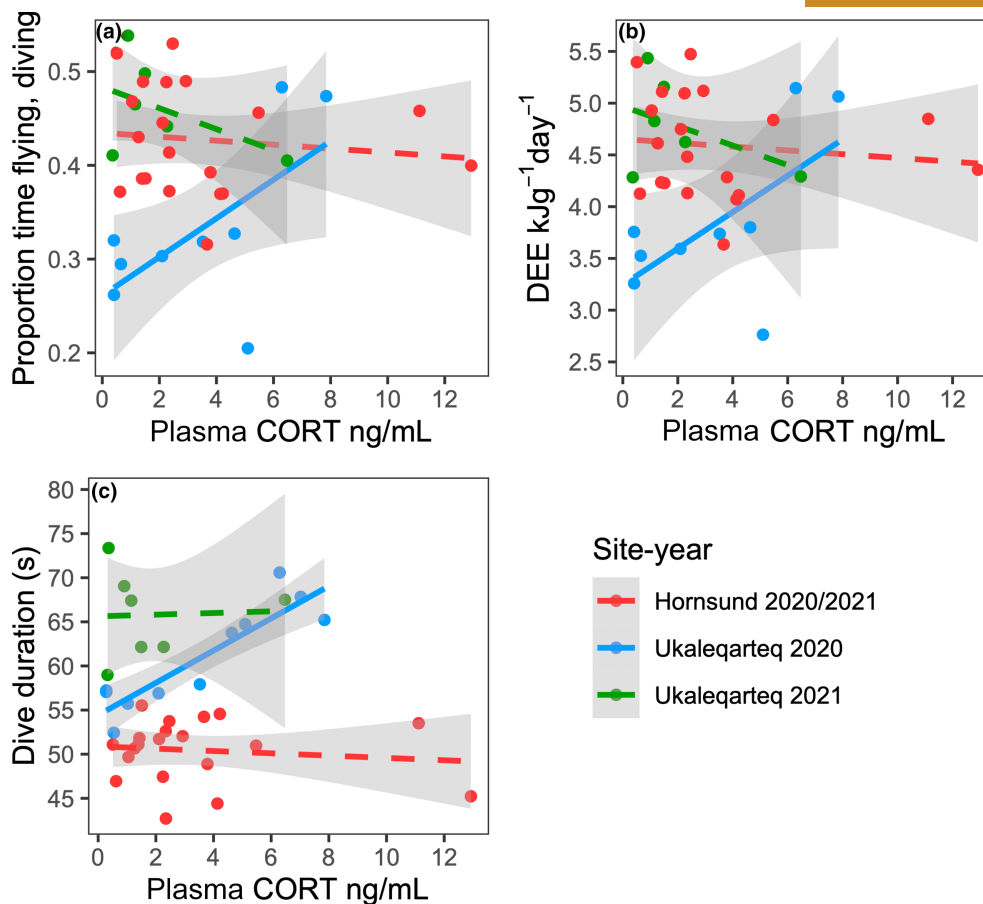


FIGURE 1 Site-year-dependent relationships between little auk baseline corticosterone (CORT) and (a) proportion time flying/diving (time activity budget; TAB), (b) daily energy expenditure (DEE) and (c) dive duration. Solid lines indicate significant relationships. For TAB/DEE, sample sizes: 9, 6 and 20 birds for Ukaleqarteq 2020, Ukaleqarteq 2021 and Hornsund (data for 2 years combined). For dive duration, sample sizes: 11, 7, 20.

TABLE 3 Linear model for relationship between little auk baseline corticosterone ($CORT_b$) and daily energy expenditure (DEE) across site-years. Ukaleqarteq 2020 is the reference. Sample sizes: 9, 6 and 20 for Ukaleqarteq 2020, Ukaleqarteq 2021 and Hornsund (data for 2 years combined).

Variable	$\beta \pm SE$	T_{29}	p	$F_{1/2,29}$	p
Intercept	3.803 ± 0.182	29.258	<0.001		
$CORT_b$	0.516 ± 0.206	2.498	0.018	0.029	0.865
Hornsund	0.792 ± 0.219	3.612	0.001	7.280	0.002
Ukaleqarteq 2021	0.865 ± 0.310	2.793	0.009		
$CORT_b \times \text{Hornsund}$	-0.570 ± 0.235	-2.420	0.022	3.489	0.044
$CORT_b \times \text{Ukal. 2021}$	-0.794 ± 0.381	-2.085	0.046		

$F_{5,29} = 4.314, p = 0.004, R^2 = 0.328$

at Hornsund [4.59 ± 0.129 (4.33, 4.86)] (Figure 1b), reflecting lower activity (Table 1, Figure 1a).

3.5 | Baseline corticosterone ($CORT_b$) and diving

The relationship between dive duration and $CORT_b$ depended on site-year (significant interaction; Table 4, Figure 1c). Interactions involving mercury (Hg) and SMI were nonsignificant (Table S6). Deep

dive duration correlated positively with $CORT_b$ within Ukaleqarteq 2020 ($\beta \pm SE = 5.394 \pm 0.889, t_9 = 6.062, p < 0.001, R^2 = 0.78$), but not Ukaleqarteq 2021 ($\beta \pm SE = 0.276 \pm 0.304, t_5 = 0.091, p = 0.931, R^2 = -0.198$), or Hornsund ($\beta \pm SE = -0.387 \pm 0.752, t_{18} = -0.515, p = 0.613, R^2 = -0.040$). For Ukaleqarteq 2020, birds with the lowest CORT (0.40 ng/mL) were predicted to have dives averaging 55.1 s, and birds with the highest (6.3 ng/mL) dives averaging 65.9 s, a difference of 10.8 s. $CORT_b$ and inter-dive duration were unrelated ($p > 0.20$).

Variable	$\beta \pm SE$	T_{29}	p	$F_{1/2,32}$	p
Intercept	60.16 ± 1.136	52.961	<0.001		
CORT _b	5.394 ± 1.227	4.395	<0.001	0.185	0.670
Hornsund	-9.686 ± 1.411	-6.865	<0.001	57.18	<0.001
Ukaleqarteq 2021	5.759 ± 2.027	2.841	0.007		
CORT _b × Hornsund	-5.782 ± 1.454	-3.977	<0.001	8.012	0.001
CORT _b × Ukal. 2021	-5.118 ± 2.428	-2.108	0.042		

$F_{5,32} = 26.12, p < 0.001, R^2 = 0.772$

3.6 | Baseline corticosterone (CORT_b) and chick provisioning

Little auk CORT_b and provisioning rate were unrelated, with a non-significant CORT_b × site-year interaction ($F_{2,31} = 0.717, p = 0.496$) and main effect ($\beta \pm SE = -0.111 \pm 0.182, t_{33} = -0.608, p = 0.547$). Provisioning varied with site-year ($F_{2,32} = 5.341, p = 0.010$), being higher for Hornsund [2.87 ± 0.201 (2.465, 3.280)] and Ukaleqarteq 2020 [2.81 ± 0.300 (2.199, 3.420)] than Ukaleqarteq 2021 [1.54 ± 0.367 (0.789, 2.29)]. Birds with higher energy expenditure (DEE) provisioned at higher rates ($\beta \pm SE = 0.659 \pm 0.252, t_{31} = 2.606, p = 0.014$).

3.7 | Phylogenetically controlled analysis

In our first model, baseline corticosterone (CORT_b) was unrelated to breeding stage (Table 5a,b, Figure 2a). CORT_b negatively correlated with breeding latitude, which was unexpected, as DEE is predicted to increase with latitude (Table 5a,b, Figure 2b). Maximum longevity and clutch size were unrelated to CORT_b (Table 5a). Results were likewise nonsignificant for current brood value [mean (95% CI): -0.058 (-0.258, 0.160)].

When directly relating CORT_b to DEE, we found no CORT_b-DEE relationship (Table 5a,b, Figure 2c). The only significant predictor of CORT_b was SST, with CORT_b higher in seabirds breeding at warmer SST (Table 6). Air temperature (T_a) tended to positively predict CORT_b, but the 95% CI overlapped zero [mean (95% CI): 0.23 (-0.004, 0.468)]. We found some indication of higher CORT_b in males and lower CORT_b in larger species. Models with the lowest DICs contained these variables, but 95% CIs overlapped zero (Tables 5b and 6b).

4 | DISCUSSION

4.1 | Little auk baseline corticosterone (CORT_b), TAB and DEE

Results support environment-dependent relationships between little auk CORT_b, TAB and DEE. CORT_b during chick rearing positively correlated with time in costly behaviours and DEE only at Ukaleqarteq during 2020, when air (T_a) and SST were low and CORT_b

TABLE 4 Linear model for relationship between little auk baseline corticosterone (CORT_b) and dive duration across site-years. Ukaleqarteq 2020 is reference. Sample sizes: 11, 7 and 20 birds for Ukaleqarteq 2020, Ukaleqarteq 2021 and Hornsund (data from 2 years combined).

TABLE 5 Phylogenetically controlled Bayesian LMM predicting breeding seabird baseline corticosterone (CORT_b) from latitude, life history variables [lifespan (Max lifespan), clutch size (Max clutch)], breeding stage (brooding as reference) and sex (females as reference). (a) Full model and (b) Model with lowest DIC. Data from 104 studies, 41 species, 54 colonies.

Variable	Estimates (mean)	Lower CI (2.5%)	Upper CI (97.5%)
(a) Full model (DIC=401.79)			
Intercept	2.013	1.284	2.788
Latitude	-0.323	-0.536	-0.107 ^a
Mass	-0.016	-0.136	0.102
Max lifespan	-0.041	-0.143	0.060
Max clutch	-0.119	-0.297	0.067
Stage creche	0.189	-0.014	0.396
Stage incubation	-0.214	-0.462	0.041
Sex male	0.103	-0.007	0.211
Sex unknown	-0.143	-0.374	0.088
Phylogenetic variance	0.642	0.147	1.648 ^a
Residual variance	0.392	0.177	0.694
(b) Model with lowest DIC (DIC=397.98)			
Intercept	1.973	1.160	2.806
Latitude	-0.292	-0.507	-0.074 ^a
Mass	-0.238	-0.494	0.026
Sex male	0.103	-0.006	0.213
Sex unknown	-0.153	-0.383	0.076
Phylogenetic variance	0.809	0.242	1.890 ^a
Residual variance	0.363	0.163	0.649

^a95% CI not overlapping zero.

was elevated. Low temperatures can elevate CORT_b in association with increased resting metabolic rate (RMR) and energetic challenge (Jimeno et al., 2018). Although cold SST can favour energy-rich copepods (Amélineau et al., 2019), temporal lag in phytoplankton productivity might have limited copepod abundance during chick rearing at Ukaleqarteq in 2020, which was exceptionally cold. Conversely, exceptionally warm conditions in 2021 were also expected to disfavour copepods (Grunst, Grunst, Grémillet, Kato, Bustamante, Albert, Brisson-Curadeau, Clairbaux, Cruz-Flores, Gentès, Grissot, et al., 2023b). Higher DEE and flight times, but lower provisioning,

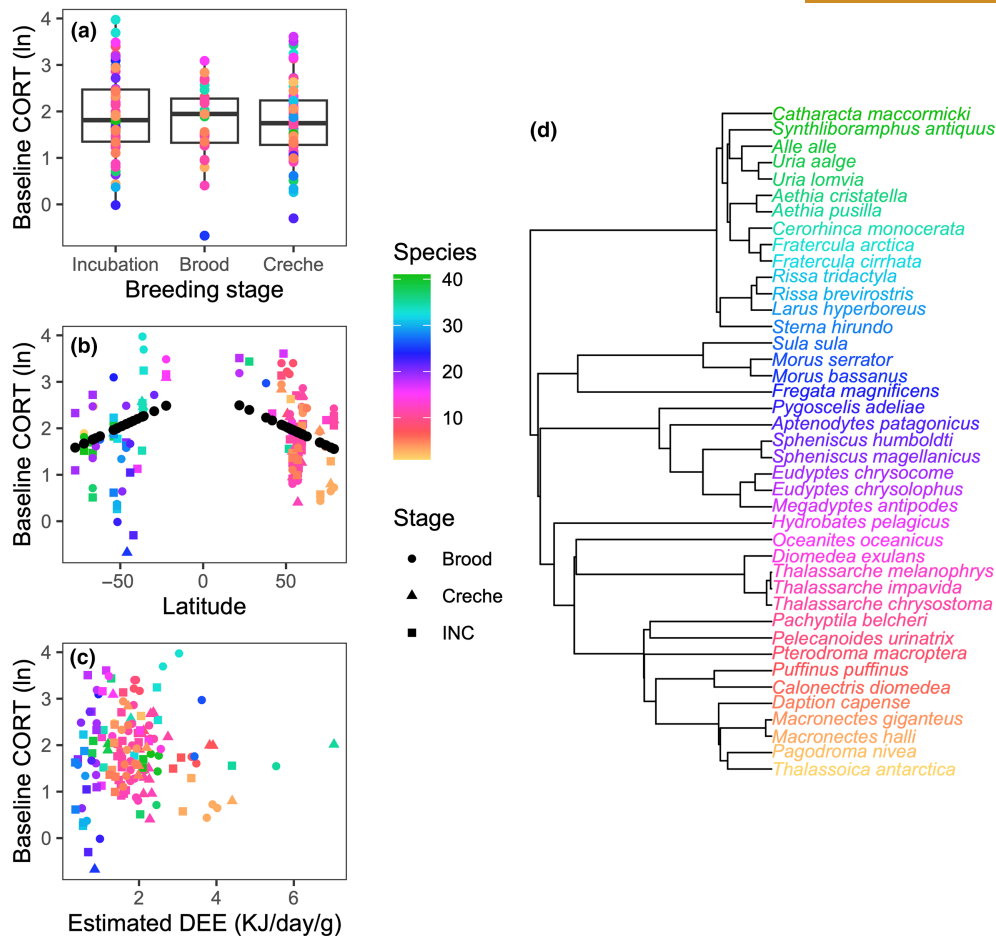


FIGURE 2 Relationships between baseline corticosterone ($CORT_b$; natural-log) across seabird species and (a) breeding stage, (b) latitude (black points are predicted values) and (c) daily energy expenditure (DEE). In (d), a phylogeny of 41 species in our dataset is shown, with species colour coded. Stages are as follows: Brood: Early chick, Creche: Late chick, INC: Incubation. Values for graphing were averaged across sexes and years within populations. $CORT_b$ data from 104 studies, 41 species, 54 colonies. DEE estimated for each colony using modelling.

in 2021 suggest that little auks ranged farther due to resource shortage. Nonetheless, energy balance might have been more challenged in 2020, due to cold temperatures and delayed productivity combined with greater parental investment, as suggested by faster provisioning. Birds that maintained high activity at Ukaleqarteq in 2020 may have been exposed to increased thermoregulatory and nutritional challenges, driving positive correlations between $CORT_b$, activity and DEE. Results are consistent with the CORT-adaptation hypothesis, as higher $CORT_b$ could have supported reproductive effort via elevated DEE. $CORT_b$ positively correlated with chick provisioning in common guillemots (*Uria aalge*) in a season when a key prey species' (capelin, *Mallotus villosus*) arrival lagged behind hatching (Doody et al., 2008). Although we found a nonsignificant correlation between $CORT_b$ and provisioning, this does not preclude effects on other parental performance metrics, as discussed below.

Multiple environmental variables (temperature, productivity) differed between years at Ukaleqarteq. More research is needed to clarify which of these are important to affecting relationships between $CORT_b$, TAB and DEE. Moreover, future studies should quantify RMR, for instance by using thyroid hormones as a proxy,

as adjusting RMR can alter energy budgets. For instance, birds with high activity could employ compensation energy management, downregulating RMR to reduce DEE (Welcker et al., 2015). However, because little auk flying and diving costs are $\sim 8 \times$ RMR, RMR contributes minimally to DEE during activity intensive chick rearing.

Little auk $CORT_b$ also correlated positively with dive duration only within Ukaleqarteq 2020. Long dives in cold water could increase $CORT_b$, reflecting thermal stress (Jimeno et al., 2018). Concurrently, elevated $CORT_b$ could facilitate diving in cold waters. CORT-implanted Adélie penguins (*Pygoscelis adeliae*) exhibited longer dives, although also prolonged resting (Cottin et al., 2011). $CORT_b$ could support long dives in cold water by upregulating metabolism and heat generation, as thermoregulation can constrain diving (Grémillet et al., 2001). On the other hand, dive durations may be oxygen limited, and lengthened by suppressing metabolic rate (Favilla & Costa, 2020). However, elevated $CORT_b$ might allow re-establishment of thermal homeostasis by elevating post-diving metabolism. Indeed, little auk body temperature declines during diving, but subsequently increases during resting on sea ice (Grunst, Grunst, Grémillet, Kato, Gentès, & Fort, 2023c). In poorly insulated Arctic

TABLE 6 Phylogenetically controlled Bayesian LMM predicting breeding seabird baseline corticosterone ($CORT_b$) from estimated daily energy expenditure (DEE; $KJday^{-1}g^{-1}$), life-history variables [lifespan (Max Life), clutch size (Max clutch)] and environmental variables (SST = sea surface temperature, CHL = chlorophyll A). (a) Full model and (b) model with lowest DIC. Data from 104 studies, 41 species and 54 colonies.

Variable	Estimates (mean)	Lower CI (2.5%)	Upper CI (97.5%)
(a) Full model (DIC=250.12)			
Intercept	1.990	1.455	2.574
Estimated DEE	-0.031	-0.188	0.128
Mass	-0.189	-0.439	0.072
SST	0.364	0.151	0.575 ^a
CHL	0.026	-0.154	0.206
Max lifespan	-0.151	-0.295	0.010
Max clutch	0.126	-0.039	0.311
Sex male	0.139	-0.006	0.283
Sex unknown	-0.042	-0.268	0.184
Phylogenetic variance	0.305	0.006	1.051
Residual variance	0.579	0.332	0.914
(b) Model with lowest DIC (DIC=248.31)			
Intercept	1.982	1.320	2.657
SST	0.340	0.123	0.558 ^a
Mass	-0.212	-0.472	0.059
Sex male	0.139	-0.005	0.284
Sex unknown	-0.052	-0.278	0.174
Phylogenetic variance	0.526	0.296	0.845 ^a
Residual variance	1.983	1.320	2.657

^a95% CI not overlapping zero.

great cormorants (*Phalacrocorax carbo*), thermoregulation constrains dive duration and depth (Grémillet et al., 2001). Similar effects could occur in little auks and other small seabirds with high surface to volume ratios. Moreover, a recent biophysical model shows that size, shape and thermoregulatory costs predict $CORT_b$ across avian species, suggesting that CORT may be upregulated in small birds under thermal challenge (Rubalcaba & Jimeno, 2022).

Little auk $CORT_b$ was not significantly related to chick provisioning. Thus, results support context-dependent relationships between $CORT_b$, DEE and behaviour, but not direct connections to fitness-related traits. Provisioning correlated positively with DEE, suggesting that effects of $CORT_b$ on DEE within Ukaleqarteq 2020 could have supported reproductive effort. However, individuals could partition foraging effort differently between self-foraging and provisioning chicks. Therefore, $CORT_b$ could correlate with DEE, which is strongly influenced by foraging effort, without relating to provisioning. Similarly, $CORT_b$ could correlate with unmeasured parental performance metrics, such as food load quality, which can vary with effort devoted to self- versus parental foraging (Grissot et al., 2019).

Past studies have reported positive, negative and null relationships between $CORT_b$, provisioning, and other reproductive performance metrics (Bonier, Martin, et al., 2009a; Bonier, Moore, et al., 2009b; Schoenle et al., 2021; Sorenson et al., 2017). Consistent with our findings, these variable results suggests that such relationships are context-dependent.

We found no evidence that Hg contamination suppresses CORT (Franceschini et al., 2009), and no relationship between $CORT_b$ and SMI. Given limited effects of Hg on the HPA axis, physiological and behavioural effects of Hg might involve other hormonal axes (Chastel et al., 2022). Lack of a $CORT_b$ -SMI relationship is surprising, as many studies report that $CORT_b$ increases as energy reserves and resources decline (Kitaysky et al., 2007). SMI is championed as a better metric of energy reserves than other condition indices (Peig & Green, 2009) but may fail to indicate energetic status under some conditions. Alternatively, long-lived little auks may avoid increases in DEE and $CORT_b$ that would compromise SMI.

4.2 | No association between baseline corticosterone ($CORT_b$) and DEE across breeding seabird species

We found no $CORT_b$ -DEE relationship across breeding seabirds, suggesting that species with higher DEE during breeding have not evolved elevated $CORT_b$ to support costs. Rather, $CORT_b$ might reflect environmental conditions that affect energy balance, with $CORT_b$ -DEE correlations emerging on an environment-dependent basis, as in our empirical dataset. Furthermore, DEE might vary with environmental conditions within colonies. We could not assess such variation due to modelling limitations. However, as the model predicted empirical DEE data well, we would expect to detect a $CORT_b$ -DEE correlation given a strong, evolved relationship between them.

Our little auk data suggest that temperature affects $CORT_b$ and $CORT$ -DEE correlations. Seabird researchers have shown that resources also affect $CORT_b$ (Kitaysky et al., 2007). Therefore, high $CORT_b$ in tropical species might reflect resource or heat stress (Catry et al., 2013; Cook et al., 2020), but more data are needed to assess causation. In contrast, an analysis from passerines found higher $CORT_b$ at high latitudes, where reproduction is intense across short seasons (Hau et al., 2010). Thus, positive $CORT_b$ -DEE relationships could occur among breeding birds, or other animals, that are shorter lived than seabirds.

5 | CONCLUSIONS

Data from little auks suggest environment-dependent relationships between baseline corticosterone ($CORT_b$) during reproduction, behaviour and DEE, whereas our phylogenetically controlled analysis suggests that seabird species with high DEE during breeding have not co-evolved seasonally elevated $CORT_b$. Rather, $CORT_b$ during breeding appeared elevated in tropical seabirds, contrary

to patterns in passerines. Overall, results suggest that $CORT_b$ in breeding seabirds depends on nutritional and thermal challenges affecting energy balance, rather than DEE alone, with $CORT_b$ -DEE correlations being context-dependent. In little auks, results suggest that $CORT_b$ might support DEE and diving under thermal or nutritional challenge. Findings support an environment-dependent understanding of the CORT-adaptation hypothesis, as capacity to elevate DEE under environmental challenge may enhance fitness. More research is needed across taxa to elucidate environmental and life-history contexts that promote correlations between $CORT_b$, DEE and fitness.

AUTHOR CONTRIBUTIONS

A.S.G. conceived of the study design, analysed data and wrote the first draft of the manuscript. M.L.G. aided in the phylogenetically controlled analysis, including the literature review and in writing. J.F., D.G., K.W.J. and D.J. helped to develop the conceptual framework and led complex fieldwork initiatives. O.C. and C.P. led corticosterone assays and granted insight regarding corticosterone's energetic and behavioural roles. M.C-F., S.G. and A.G. were instrumental in data collection and management. All authors played important roles in revisions and approved the final version of the manuscript.

ACKNOWLEDGEMENTS

We acknowledge support from the European Union's Horizon 2020 programme (Marie Skłodowska-Curie IFs 896866, 101025549, 101024166), and long-term funding from the French Polar Institute (IPEV) to the ADACLIM program (388) administered by J.F. and D.G. Thanks to Maud Brault-Favrou of the platform Analyses ELémentaires de LIENSs laboratory for assistance with Hg analyses, and Marie Pallud of the Service d'Analyses Biologiques of CEBC for assistance with CORT analyses. This work contributes to the projects ARCTIC-STRESSORS and ILETOP funded by the French National Research Agency (ANR-20-CE34-0006, ANR-16-CE34-0005), international ARCTOX initiative, Excellence Chair ECOMM funded by Region Nouvelle Aquitaine and OPUS13 funded by the Polish National Science Center (2017/25/B/NZ8/01417).

CONFLICT OF INTEREST STATEMENT

David Grémillet is an Associate Editor of Functional Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data are accessible via Zenodo: <https://doi.org/10.5281/zenodo.12658832> (Grunst et al., 2024).

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SUPPORTING INFORMATION

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

Appendix S1. Estimating DEE from TABs.

Appendix S2. Literature search methodology and results.

Table S1. Studies and data used in phylogenetic analysis.

Appendix S3. Deriving environmental and life-history data.

Tables S3–S7. Supplementary statistical results.

How to cite this article: Grunst, A. S., Grunst, M. L., Grémillet, D., Chastel, O., Cruz-Flores, M., Gentès, S., Grissot, A., Jakubas, D., Kato, A., Parteneau, C., Wojczulanis-Jakubas, K., & Fort, J. (2024). Environment-dependent relationships between corticosterone and energy expenditure during reproduction: Insights from seabirds in the context of climate change. *Functional Ecology*, 00, 1–13. <https://doi.org/10.1111/1365-2435.14630>