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RESEARCH ARTICLE

# Breeding under pressure: Corticosterone is associated with reproductive investment under fluctuating predation risk in a long-lived sea duck

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## Abstract

1. Phenotypic plasticity may enable individuals to cope with predictable and unpredictable environments during their life-cycle. In that context, studying glucocorticoids—corticosterone (CORT) in birds—is relevant because of their primary role in allostasis. Higher baseline CORT levels are classically associated with environmental constraints and lower fitness (the CORT-fitness hypothesis). However, in some environments, higher baseline CORT levels can promote reproduction, therefore being associated with higher fitness (the CORT-adaptation hypothesis). These two hypotheses have been tested in multiple systems but rarely in a context of fluctuating predation threat.

2. We used a long-term individual-based monitoring of baseline CORT levels in female common eiders *Somateria mollissima* ($n_{CORT} = 1537$; $n_{individual} = 790$; 2009–2022) to disentangle the context-dependent links between environmental conditions, CORT and fitness. Importantly, the study population has been facing a drastic increase in predation pressure over the past decades, linked to the recovery of the white-tailed eagle *Haliaeetus albicilla*. Additionally, eiders breed on open or forested islands, further affecting adult and nest predation risk. This system allowed us to disentangle the relative contributions of within- and among-individual variation in baseline CORT levels under predation.

3. Supporting the CORT-adaptation hypothesis, baseline CORT levels were positively associated with reproductive investment (clutch size), age and hatching success. By partitioning within- and among-individual effects, we showed that at the individual level, CORT flexibly increased with clutch size and age. Females displaying higher CORT levels were more successful, suggesting a link between CORT and individual quality.

4. At both the population and individual levels, baseline CORT levels decreased over the study period. This decrease was correlated with an increase in predation risk. Females had reduced baseline CORT when nesting under high eagle abundance

or adult predation risk (within-individual effect). Interestingly, apparent plasticity towards adult predation risk was only observed on open islands, likely reflecting habitat-dependent strategies.

5. Consistent with the CORT-adaptation hypothesis, we show that changes in predation regime not only correlate with changes in reproductive investment, but also with rapid plastic adjustment of glucocorticoid levels and therefore individual strategies to cope with predation risk. Given the correlative nature of our study, we encourage further experimental studies testing for a causal relationship between predation and corticosterone levels.

## 1 | INTRODUCTION

Organisms encounter predictable and unpredictable environmental challenges during their life cycle (Jacobs & Wingfield, 2000). In such dynamic contexts, selective or plastic adjustments of morphology, behaviour and physiology are predicted to maximise fitness and allow individuals and populations to persist (Chevin et al., 2010; Fierst, 2011; Taff & Vitousek, 2016; Wingfield, 2003). While organisms may have evolved life-history strategies to cope with predictable environmental changes (e.g. seasonality), unpredictable environmental fluctuations (e.g. fluctuating weather or predation pressure) require rapid phenotypic adjustments (Bonamour et al., 2019; Wingfield, 2003). Predation pressure is a major source of such unpredictable environmental perturbation, influencing both life-history traits and strategies of prey (Lima, 1998).

Under environmental constraints, the ability of individuals to complete their annual life-cycle highly depends on the mechanisms of allostasis (i.e. maintaining stability through change sensu McEwen & Wingfield, 2003; Romero et al., 2009). One of the most studied allostatic pathways is the hypothalamo-pituitary–adrenal axis, because the secretion of glucocorticoids—corticosterone (CORT) in many vertebrates—mediates several physiological and behavioural changes that aim to restore homeostasis (Angelier & Wingfield, 2013; Sapolsky et al., 2000; Wingfield & Sapolsky, 2003). Circulating glucocorticoid levels can thus fluctuate in response to challenging extrinsic or intrinsic conditions, and are thought to mirror higher energetic demands under harsh conditions (Harris, 2020; Landys et al., 2006; Wingfield, 2013). Several studies have demonstrated elevated baseline glucocorticoid levels under high predation pressure (Clinchy et al., 2004; Hik et al., 2001; Middlemis Maher et al., 2013; Noreikienė et al., 2021; Scheuerlein et al., 2001; Spong et al., 2020), or under nutritional stress, notably during years of poor or unpredictable food availability (Angelier et al., 2015; Kitaysky et al., 1999; Pravosudov et al., 2001).

The conventional view is that elevated baseline glucocorticoid levels reflect stressful conditions and are therefore negatively correlated with fitness (the CORT-fitness hypothesis, Bonier et al., 2009), but increased glucocorticoid concentrations can also promote survival and reproduction under challenging conditions (Sorenson et al., 2017; Vitousek et al., 2018), thus being positively associated with fitness (the CORT-adaptation hypothesis, Bonier et al., 2009). For example, several studies provide evidence for an association between elevated baseline glucocorticoid levels and reduced survival (Goutte, Angelier, Welcker, et al., 2010; Jimeno et al., 2018; Lancaster et al., 2008), lower breeding success (Henderson et al., 2017; Ouyang et al., 2011; Sheriff et al., 2009) or limited breeding experience (Angelier, Weimerskirch, et al., 2007), resulting in a reduction in overall fitness (Angelier et al., 2010; Buck et al., 2007). In contrast, under environmental constraints, individuals with higher glucocorticoid levels may perform better than those with lower levels (e.g. Henderson et al., 2017) because glucocorticoids can promote foraging behaviour (Angelier, Shaffer, et al., 2007; Crossin et al., 2012), metabolic activities (Jimeno et al., 2018), parental care (Crossin et al., 2012; Silverin, 1982) and even morphological changes reducing the risk of predation (Middlemis Maher et al., 2013). Consequently, a few studies have reported elevated glucocorticoid levels in breeders laying larger or heavier clutches (Kouwenberg et al., 2013), and in those that are more committed to incubation (Ouyang et al., 2013), successful at hatching a clutch (Crossin et al., 2013; Fischer et al., 2020; Riechert et al., 2014), or older and more experienced (Angelier et al., 2006; Carlitz et al., 2022), supporting the idea that higher baseline glucocorticoid levels facilitate current reproduction (Bonier et al., 2009).

The relationship between baseline glucocorticoids and fitness under variable environmental conditions therefore remains debated. Long-term individual-based studies are key to determine the fitness value of traits (Clutton-Brock & Sheldon, 2010; Taff & Vitousek, 2016), and thus have the potential to inform us about how glucocorticoids relate to fitness metrics under contrasting environments (Bonier & Martin, 2016). To this end, we combined a traditional correlative approach with the within-subject centering method (van de Pol & Wright, 2009), to distinguish among-individual

responses from within-individual endocrine plasticity across variable environments (Grindstaff et al., 2022; Guindre-Parker, 2020; Hau & Goymann, 2015). Such an approach requires repeated sampling of individuals along gradients of environmental conditions to specifically assess how individuals respond hormonally to environmental fluctuations (Grindstaff et al., 2022; Malkoc et al., 2022). Heeding this call, we here relied on a long-term (2009–2022) individual-based monitoring of baseline CORT levels of incubating female common eiders *Somateria mollissima*—hereafter, eiders—facing an unprecedented increase in predation pressure (Öst et al., 2022), to investigate how individuals adjust CORT levels to fluctuating predation threat.

The focal eider population has witnessed a dramatic shift in predation regime—mainly linked to the recovery of eiders' most important native predator, the white-tailed eagle *Haliaeetus albicilla* (Ekblad et al., 2016). The Baltic white-tailed eagle population was at the brink of extinction during the mid-20th century until the 1970s, primarily due to human persecution and environmental pollution, but has since then grown rapidly owing to effective conservation efforts (Hipfner et al., 2012; Treinys et al., 2016). Both breeding and non-breeding eagles are now abundant and roam across the entire study area irrespective of island type or isolation (Supplementary Material S1). Such ongoing increase in white-tailed eagle abundance may profoundly affect seabird populations (Anker-Nilssen et al., 2023; Hipfner et al., 2012), but the extent to which prey populations can cope with this rapid change in predation regime still deserves further research.

We thus assessed (1) whether the dramatic shift in predation regime is associated with population-level changes in baseline CORT and hatching success. At the individual level, we investigated (2) the intra-individual consistency of baseline CORT levels (i.e. repeatability) and the relationship between baseline CORT, predation risk,

reproductive investment and hatching success. Finally, we explored (3) whether individual variation in baseline CORT in response to fluctuating predation risk and reproductive investment was shaped by within-individual plasticity or among-individual effects.

We formulated two contrasting predictions based on the CORT-fitness and CORT-adaptation hypotheses, respectively (Figure 1). Under the CORT-fitness hypothesis (Prediction 1), we expected higher baseline CORT in younger females, those in poorer body condition, investing less in current reproduction—that is laying smaller clutches—or failing in their breeding attempt. We also predicted that higher predation risk—that is years of high predator abundance, islands with high adult or nest predation, or less sheltered habitats—would be associated with both population- and individual-level increases in CORT. In contrast, under the CORT-adaptation hypothesis (Prediction 2), we expected baseline CORT levels to be higher in older females, those in better condition or investing more in current reproduction—that is laying larger clutches—or breeding successfully. Accordingly, we predicted that the temporal increase in predation risk would be associated with a population- and individual-level decrease in reproductive investment, which would be accompanied by a concomitant decrease in baseline CORT levels.

## 2 | MATERIALS AND METHODS

### 2.1 | Female eider monitoring

Eiders were monitored in a colony surrounding Tvärminne Zoological Station (59°50′N, 23°15′E) in southwestern Finland (Baltic Sea). There, female eiders breed on open islands characterised by bare rocks and low vegetation cover ($n = 13$ islands, mean vegetation cover $\pm$ SD: 3.7% $\pm$ 5.6%, range: 0%–15.4%) or
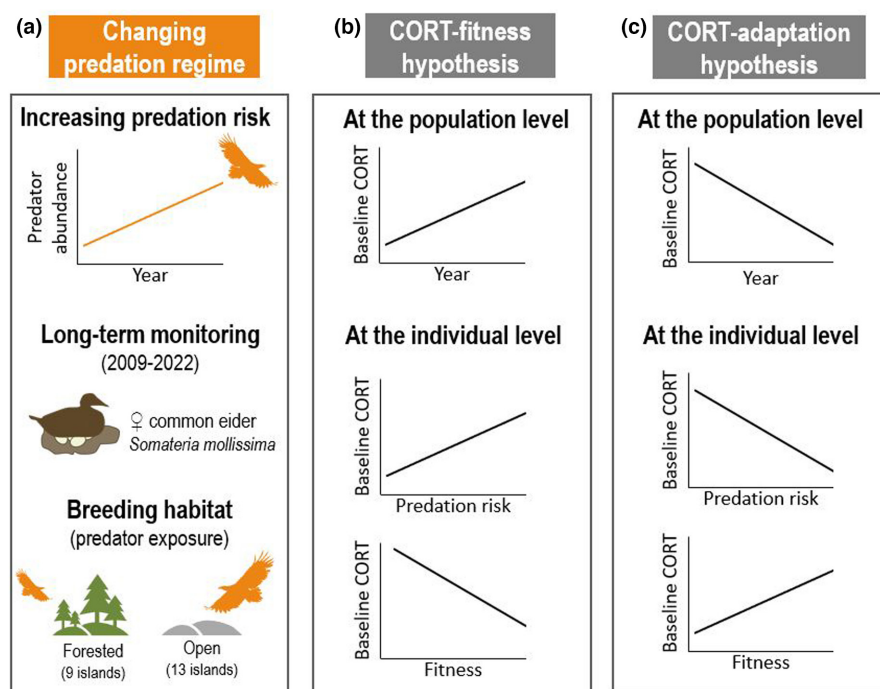


**FIGURE 1** (a) Around Tvärminne, female common eiders face the recovery of their main predator, the white-tailed eagle. In the study area, female eiders breed on forested islands, where nests are concealed from predator sight, or on open islands, where nests are more conspicuous to predators. We derived two sets of predictions linking baseline corticosterone levels, predation risk and fitness, following either (b) the CORT-fitness or (c) the CORT-adaptation hypothesis.

on forested islands dominated by pine forest ($n = 9$ islands, mean vegetation cover $\pm$ SD: $43.2\% \pm 7.2\%$, range: $30.9\%$–$53.0\%$). The study islands are part of a nature reserve and visits are only allowed for research purposes, limiting human disturbance to a minimum. A team of three researchers carrying hand nets thoroughly covered the monitored islands, walking 2–5 m away from each other, aiming to detect and catch all incubating female eiders as well as to detect carcasses of dead females and depredated nests. Monitoring was carried out between mid-May and early June, a period corresponding to late incubation stage in this eider population, to minimise the risk of nest abandonment following disturbance (Bolduc & Guillemette, 2003). Bird handling was approved by the Finnish Project Authorization Board of the Regional Administrative Agency for Southern Finland (permit numbers ESAVI/1697/04.10.03/2012; ESAVI/2831/04.10.07/2015; ESAVI/4053/2018; ESAVI/10022/2021) and complied with the regulations of Tvärminne Zoological Station.

Between 2009 and 2022, 1537 incubating female eiders ($n_{individual} = 790$, see further details in Supplementary Material S2) were trapped on their nest between 9:00 AM and 7:30 PM. Eiders are long-lived birds characterised by a mean life expectancy of 11.8 years (95% confidence interval: [5.4–25.2]; Wood et al., 2020). In the study area, females have been ringed with a unique metal ring when caught breeding for the first time since 1990. High trapping success and constant trapping effort allow us to use the number of years since ringing as a proxy of female minimum age (see Jaatinen & Öst, 2011). Females were weighed to the nearest 10 g and the radius-ulna length—a proxy of structural body size—was measured to the nearest 1 mm. To assess available body reserves at the time of trapping, we calculated a body condition index by standardising the residuals of a linear regression of log-transformed body weight on log-transformed radius-ulna length (Jakob et al., 1996). We also calculated body condition following Peig and Green (2009). The two body condition indices were correlated ($r = 0.59$, $p < 0.001$) and provided similar results.

Clutch size was recorded during female handling as a proxy of initial reproductive investment (Hanssen et al., 2003, 2022; Jaatinen et al., 2013). Egg floatation was used to estimate incubation stage (mean number of days of incubation $\pm$ SD $= 17 \pm 5$ days, range $= 5$–24 days) and associated laying and hatching dates (in days since April 1) (Kilpi & Lindström, 1997). Egg floatation is based on the principle that as eggs gradually lose weight due to water loss and the development of an air cell, a concomitant decline in egg specific gravity occurs, from a gravity greater than water to a specific gravity lower than water. We calculated individual relative laying date (in days) by centring laying date around the yearly median laying date of the entire population (including nests of both untrapped and trapped females), to allow comparison of individual breeding timing irrespective of annual phenology.

Eider incubation lasts on average 26 days (Korschgen, 1977). Nests were revisited on the predicted hatching date to measure hatching success (0: failure, 1: success, $n = 1457$ revisited nests). Duckling presence in the nest indicated hatching success. However, because the precocial ducklings leave the nest within a day of hatching (Öst & Bäck, 2003), eggshells and membranes were inspected to evaluate hatching success in the absence of ducklings. Intact leathery membranes were typically found if ducklings had successfully hatched, while broken shell pieces with bloody membranes or shell absence indicated nest depredation. The breeding attempt was considered successful if at least one duckling or one leathery membrane was found in the nest.

## 2.2 | Baseline CORT sampling and assay

The 1537 monitored females were sampled for blood from the ulnar vein (~1.5 mL) within 3 min of capture (mean $\pm$ SD $= 2.38 \pm 0.40$ min, range $= 1.17$–2.98 min), a sampling time allowing the measurement of baseline CORT concentrations (Romero & Reed, 2005). Samples were centrifuged and blood serum was stored at −20°C until CORT radioimmunoassay was carried out at the Centre d'Etudes Biologiques de Chizé (mean inter-assay coefficient of variability (CV): 13.66%, mean intra-assay CV: 8.98%). This radioimmunoassay method is further detailed in Supplementary Material S3 and has been validated for the study population (Mohring et al., 2021; Öst et al., 2020). As baseline CORT levels (in ng/mL) did not significantly increase with sampling time (linear regression of baseline CORT levels on sampling time, including year to control for interannual variation in baseline CORT levels: $t = 0.82$, $p = 0.41$) and as all samples were taken within 3 min (Romero & Reed, 2005), they were considered to reflect baseline levels and hence we did not include sampling time in the following statistical analyses. Measured baseline CORT concentrations are in the same range as those assayed from other eider populations during incubation (Bourgeon & Raclot, 2006; Criscuolo et al., 2006; D'Alba et al., 2011). As baseline CORT levels also did not significantly vary with time of day (linear regression of baseline CORT levels on time of day, including year: $t = -1.29$, $p = 0.20$) or between morning and afternoon (linear regression of baseline CORT levels on period of day, including year: $t = 1.07$, $p = 0.28$), we did not include time of sampling in the following analyses.

## 2.3 | Quantifying predation pressure

In the study area, adult female eiders are primarily depredated by white-tailed eagles, as well as by American minks *Neovison vison* and raccoon dogs *Nyctereutes procyonoides* (Öst et al., 2018). Importantly, mammalian predators have been controlled in the study area since 2011, thanks to an invasive alien predator removal scheme (Jaatinen et al., 2022). Eider eggs are either consumed by primary predators of adult eiders, or by hooded crows *Corvus cornix* or gulls *Larus* spp. (whose populations are stable or decreasing, respectively, in the study area; Hermansson et al., 2023), in most cases when the female is absent from the nest (Jaatinen et al., 2014).

To quantify eagle activity in the landscape during the eiders' reproductive season, we calculated an annual index of white-tailed eagle abundance in the study area during this time. This index was calculated, for each year, as the average daily number of white-tailed eagle sightings between April 1 and June 15 at the nearby (ca 20 km) Hanko Bird Observatory (HALIAS, 59°49′ N, 22°54′ E) (Öst et al., 2022). Following the HALIAS protocol, 1–6 observers counted the number of resident eagles (both potential breeders and highly mobile subadults) during a 4-h standardised period beginning at sunrise each day (Lehikoinen et al., 2008). These standardised counts are coordinated by an observer with decades-long experience, which reduces the risk of double counting the same individual.

We also measured island-specific yearly indices of predation risk encompassing predation events from all potential predators of adults and their eggs. For each year and island, island-specific adult predation risk index was calculated by dividing the number of killed females on a given year and island by the total number of breeding attempts on this island and year. Female carcasses and remains were examined to verify that they died from a predator attack and to identify the predator species (Öst et al., 2018). Actively incubated, depredated and already hatched nests during female monitoring were defined as breeding attempts. Because nest and adult predation are distinct processes that can trigger different antipredator responses (Hua et al., 2014; Mohring et al., 2022), we also calculated an island-specific nest predation risk index. For each island and year, island-specific nest predation risk index was calculated by dividing the number of failed breeding attempts on a given year and island by the total number of breeding attempts for which nest fate was known, on this island and during this year (4156 known nest fates out of 4501 nests, 92.3%). Egg depredation was the main cause of failed breeding attempts but abandoned nests or unviable clutches were occasionally found (2201 depredated nests out of 2421 failed breeding attempts, 90.9%).

## 2.4 | Statistical analyses

Statistical analyses were conducted in R 4.0.4. (R Core Team, 2021). We implemented linear models (LMs), linear mixed models (LMMs) and generalised linear mixed models (GLMMs) (R functions 'lmer' and 'glmer', lme4 package; Bates et al., 2015). Baseline CORT as a dependent variable was $\ln(x+1)$ transformed to meet model assumptions, and we visually verified that the assumptions of normality and homoscedasticity of residuals were met in selected models (Zuur et al., 2009, 2010). In addition, quantitative independent variables were centred and scaled. Fixed effect parameter estimates ($\beta$) and their 95% credible intervals (CI) were estimated from posterior distributions of 10,000 simulations (R function 'sim', arm package; Gelman & Su, 2021). We verified that we could not detect multicollinearity among the variables included in final selected models (all variance inflation factors, VIFs <2.1, that is below the conservative threshold of 2.5; Allison, 2012).

### 2.4.1 | Temporal trends in CORT, predation risk and hatching success

Because of temporal variation in independent variables, we assessed temporal trends in baseline CORT levels and investigated the relationship between baseline CORT, predation risk and reproductive investment in separate models to prevent collinearity issues. Hence, we built a LMM with baseline CORT as the dependent variable, year as the independent variable and individual identity as a random effect. Similarly, we assessed temporal variation in predation risk using a LM and LMMs with yearly eagle index (LM), island-specific adult and nest predation risk (LMMs) as dependent variables, year as an independent variable, and island identity as a random effect in LMMs. Last, we assessed the temporal trend in hatching success using a GLMM with a binomial error distribution with hatching success as the dependent variable, year as the independent variable and female identity as a random effect.

### 2.4.2 | Baseline CORT levels

First, we estimated individual repeatability in baseline CORT levels (R function 'rpt', rptR package; Stoffel et al., 2017). Then, we built LMMs with baseline CORT levels as the dependent variable ($n=1537$) and female age, its quadratic term (to investigate potential non-linear effects of age), body condition, clutch size, island type (open/forested), relative laying date, eagle index, and island-specific adult and nest predation risk as independent variables, and female identity and year as random effects. Because we expected habitat-specific responses to predation threat, interactions between island type and predation risk indices were also included. All possible combinations of the aforementioned variables were computed and run using 'dredge' function (MuMIn package; Barton, 2020). The 'best' models were identified as the models with the lowest Akaike's Information Criterion corrected for small sample sizes (AICc; Barton, 2020) and within ΔAICc <2. Among the four top-ranked models (ΔAICc <2; Supplementary Material S4), the one with the fewest parameters was selected as the final most parsimonious model because of the known leniency of the AIC based approach in retaining model terms (Aho et al., 2014). To verify the robustness of our model selection, we additionally performed conditional model averaging across the models within ΔAICc <2 ('model.avg' function, MuMIn package; Barton, 2020). This robustness check confirmed that we had correctly identified the final model predicting variation in baseline CORT levels and the significance of each included independent variable (Supplementary Material S5).

To disentangle within-individual from among-individual effects of final selected quantitative independent variables on CORT, we relied on within-subject centering, separating these independent variables into their within- and among-individual components, relying on a within-subject centering approach (van de Pol & Wright, 2009). Within-individual components were calculated by centering values around the individual mean, while among-individual components corresponded to mean individual values of

each focal variable (eq. 2; van de Pol & Wright, 2009). We thus re-run the final selected model predicting variation in baseline corticosterone levels—including linear and quadratic female age, clutch size, island type, relative laying date, eagle index, island-specific adult predation risk and the interaction between island type and island-specific adult predation risk as independent variables, and female identity and year as random effects—by replacing each quantitative independent variable by its within- and among-individual components. We tested for quadratic age effects following eq. 3 in Fay et al. (2022). When within- and among-individual effects were both significant, we tested whether the two effects significantly differed from each other (eq. 3; van de Pol & Wright, 2009). A non-significant difference between within- and among-individual effects indicates that the effect can be attributed to within-individual plasticity (van de Pol & Wright, 2009).

### 2.4.3 | Hatching success

To evaluate the relationship between hatching success and baseline CORT levels, we built a GLMM with a binomial error distribution, with hatching success as the dependent variable (0: failure, 1: success, $n = 1457$), female baseline CORT level as the independent variable, and female identity and year as random effects. Incubation stage—the number of days since the start of incubation—was added as a covariate to control for the decreasing time window for potential predation between trapping and hatching with advancing incubation stage. To separate the effects of within- and among-individual variation in baseline CORT levels on hatching success, we built a second GLMM similar to the first one but in which we replaced baseline CORT by its within- and among- individual components (van de Pol & Wright, 2009). In this GLMM, female identity and year were included as random effects.
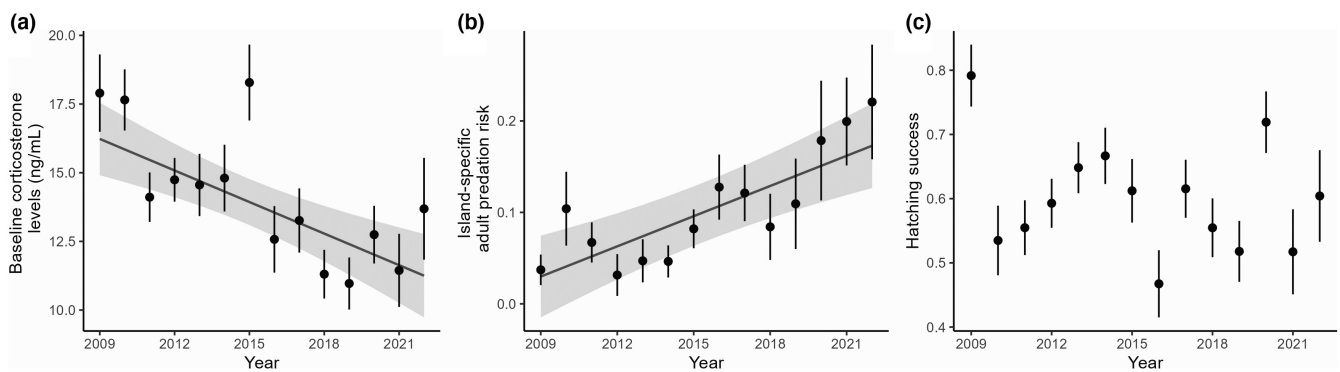


**FIGURE 2** Temporal variation in (a) incubating female common eider baseline corticosterone levels, (b) island-specific adult predation risk and (c) hatching success over the 14-year study period. Black dots correspond to yearly mean values of the focal variables and bars account for yearly standard errors. Regression lines are presented for significant temporal trends, and grey areas account for 95% confidence intervals.

**TABLE 1** Effect of individual (clutch size, female minimum age, relative laying date) and environmental independent variables (island type, white-tailed eagle abundance, island-specific adult predation risk and its interaction with island type) on variation in baseline corticosterone levels of female common eiders, including female identity and year as random effects. The 'combined within- and among-individual effects' column shows the final model selected based on AICc. The 'partitioned within- and among-individual effects' column summarises derived models in which each significant quantitative variable is partitioned into its within- and among-individual components. Parameter estimates ($\beta$) are presented with 95% credible intervals in squared brackets and in bold when excluding zero. Forested islands are used as a reference island type.

| | | Combined within- and among-individual effects | Partitioned within- and among-individual effects | |
| --- | --- | --- | --- | --- |
| | | $\beta$ [CI] | $\beta_{within}$ [CI] | $\beta_{among}$ [CI] |
| Fixed effects | | | | |
| Intercept | | **2.47 [2.39, 2.55]** | **2.47 [2.39, 2.55]** | |
| Clutch size | | **0.08 [0.05, 0.12]** | **0.04 [0.01, 0.07]** | **0.08 [0.04, 0.12]** |
| Female minimum age | $\beta_{lin}$ | **0.20 [0.14, 0.25]** | **0.15 [0.07, 0.23]** | **0.18 [0.12, 0.24]** |
| | $\beta_{sqr}$ | **−0.07 [−0.10, −0.04]** | **−0.11 [−0.18, −0.03]** | **−0.06 [−0.09, −0.03]** |
| Relative laying date | | **−0.05 [−0.09, −0.01]** | −0.01 [−0.04, 0.03] | **−0.06 [−0.10, −0.02]** |
| Eagle index | | **−0.13 [−0.19, −0.07]** | **−0.06[−0.10, −0.01]** | **−0.12 [−0.18, −0.06]** |
| Island type | $\beta_{open}$ | **0.11 [0.01, 0.21]** | **0.11 [0.01, 0.21]** | |
| Island-specific adult predation risk | | 0.02 [−0.02, 0.07] | **0.03 [0.00, 0.07]** | −0.01 [−0.05, 0.04] |
| Island type × island-specific adult predation risk | $\beta_{open}$ | **−0.15 [−0.24, −0.06]** | −0.08 [−0.17, 0.01] | **−0.12 [−0.21, −0.02]** |

Abbreviations: $\beta_{lin}$, $\beta$ for the linear age effect; $\beta_{open}$, $\beta$ for effects on open islands; $\beta_{sqr}$, $\beta$ for the quadratic age effect.

## 3 | RESULTS

### 3.1 | Temporal trends

Baseline CORT levels decreased over the study period (LMM: $\beta = -0.13$, CI$=(-0.17, -0.09)$, Figure 2a), while the three predation risk indices increased (eagle index: LM, $\beta = 2.44$, CI$=(1.78, 3.12)$, island-specific adult predation risk: $\beta = 0.04$, CI$=(0.02, 0.06)$, Figure 2b; island-specific nest predation risk: LMM, $\beta = 0.08$, CI$=(0.05, 0.11)$). We did not detect any temporal trend in hatching success (GLMM: $\beta = -0.11$, CI$=(-0.25, 0.03)$, Figure 2c).

### 3.2 | Baseline CORT levels

Baseline CORT levels were repeatable within individuals (repeatability $(R) \pm SE = 0.19 \pm 0.03$, CI$=(0.13, 0.25)$, $p < 0.001$). The final model predicting female baseline CORT levels included clutch size, female minimum linear and quadratic age, relative laying date, eagle index, island-specific adult predation risk, island type, and the interaction between island type and island-specific adult predation risk, but not body condition or nest predation risk (Table 1). Baseline CORT levels were positively associated with clutch size (Table 1, Figure 3a), with individuals displaying higher baseline
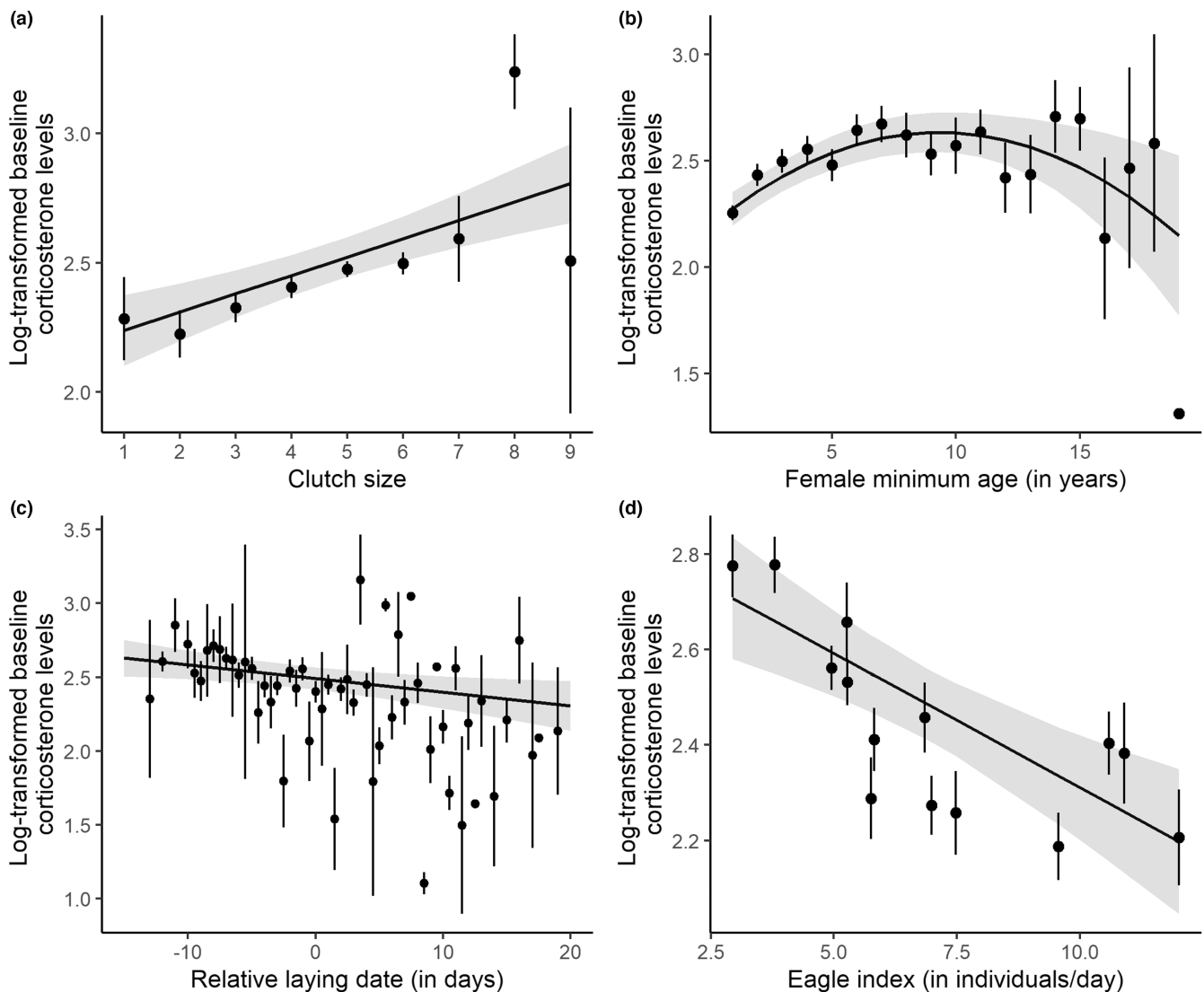


**FIGURE 3** Relationship between female common eider log-transformed baseline corticosterone levels and (a) clutch size (number of eggs), (b) female age, (c) relative laying date (female laying date centred around the yearly median laying date of the entire population to allow comparison of individual breeding timing irrespective of annual phenology) and (d) white-tailed eagle index (average daily number of white-tailed eagle sightings between April 1 and June 15 at the nearby Hanko Bird Observatory). Black dots correspond to mean values of the independent variables and bars account for standard errors. Regression lines are presented in black, and grey areas account for 95% confidence intervals. Age effects were still significant after removing the potential outlier, that is the oldest sampled individual (linear term: $\chi^2 = 45.80$, $p < 0.001$, quadratic term: $\chi^2 = 15.99$, $p < 0.001$), as was the clutch size effect after excluding clutches below 3 and exceeding 7, corresponding to potential partial nest predation and conspecific brood parasitism, respectively ($\chi^2 = 9.44$, $p = 0.002$).

CORT levels when laying larger clutches (within-individual effect, Table 1, Supplementary Materials S6 and S7). Likewise, baseline CORT levels were positively correlated with female minimum age—a pattern reversed in the oldest breeders (quadratic age effect, Table 1, Figure 3b)—and these age effects were explained by age-dependent plasticity (within-individual effect, Table 1, Supplementary Material S6). Late breeders displayed lower baseline CORT levels than early breeders (Table 1, Figure 3c), a cross-sectional effect explained by later breeders having lower CORT levels (among-individual effect, Table 1). Baseline CORT levels were negatively associated with yearly eagle abundance (Table 1, Figure 3d), through a plastic response (within-individual effect, Table 1, Supplementary Material S6). Baseline CORT levels were also negatively associated with island-specific adult predation risk, but this response was habitat-specific, being evident on open islands only (Table 1, Figure 4, Supplementary Material S6). This effect was specifically due to a plastic reduction of baseline CORT levels being associated with higher adult predation risk on open islands (within-individual effect, Table 1, Supplementary Material S6).

## 3.3 | Hatching success

Hatching success was positively associated with female baseline CORT levels ($\beta = 0.15$, CI = [0.01, 0.27], Figure 5). This effect was attributed to among-individual ($\beta_{among} = 0.17$, CI = [0.01, 0.30]) rather than within-individual variation ($\beta_{within} = 0.06$, CI = [−0.05, 0.18]) in baseline CORT levels. The probability of successful hatching also increased with advancing incubation stage at female capture, that is with a shrinking time window for potential predation ($\beta = 0.67$, CI = [0.55, 0.81]).

## 4 | DISCUSSION

In this study, we used long-term individual-based data on female eiders to investigate the relationship between CORT and fitness under fluctuating predation pressure. First, and supporting the CORT-adaptation hypothesis, we found that higher CORT levels were associated with larger clutches—a proxy of reproductive investment—and better hatching success. Second, we found that higher predation risk was associated with lower CORT levels, both at individual and population levels. Thus, female eider baseline CORT levels decreased over the 14-year study period, and this decrease was correlated with a concurrent increase in predation pressure. Additionally, we found that an increase in eagle abundance was associated with a within-individual decrease in CORT levels, highlighting a plastic response to fluctuating predation pressure. While the nature of this study is correlational, and other environmental changes may have concomitantly occurred during the study period (e.g. changes in temperature or food availability), these findings suggest that variation in CORT levels could mediate the influence of predation threat on reproductive investment and performance. Our study joins a small but growing number of studies investigating physiological adjustments through repeated sampling of individual endocrine levels and fitness outcomes along gradients of predictable and unpredictable environmental fluctuations (reviewed in Bonier & Martin, 2016; Grindstaff et al., 2022; Malkoc et al., 2022). With this approach, we provide considerable support for phenotypic plasticity
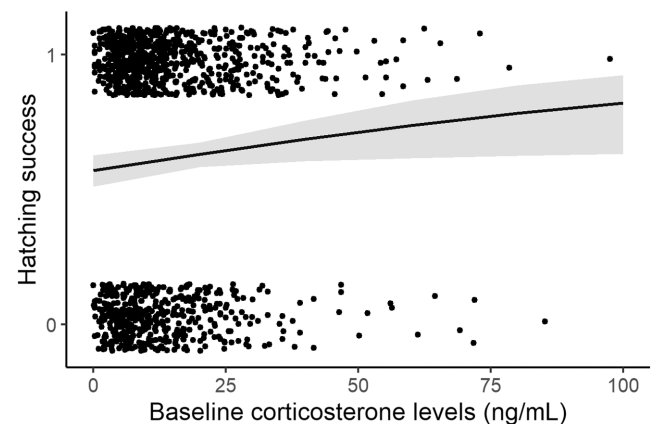
**FIGURE 5** Relationship between female common eider hatching success (0: failure, 1: success) and baseline corticosterone levels. Regression line is presented in black, and grey areas account for 95% confidence intervals.

**FIGURE 4** Relationship between incubating female common eider log-transformed baseline corticosterone levels and island type-specific adult predation risk (island-specific proportion of killed breeding females) on open and forested islands. Dots correspond to mean values of island-specific predation risk over regular intervals and bars account for standard errors. Regression lines are presented with their 95% confidence intervals.
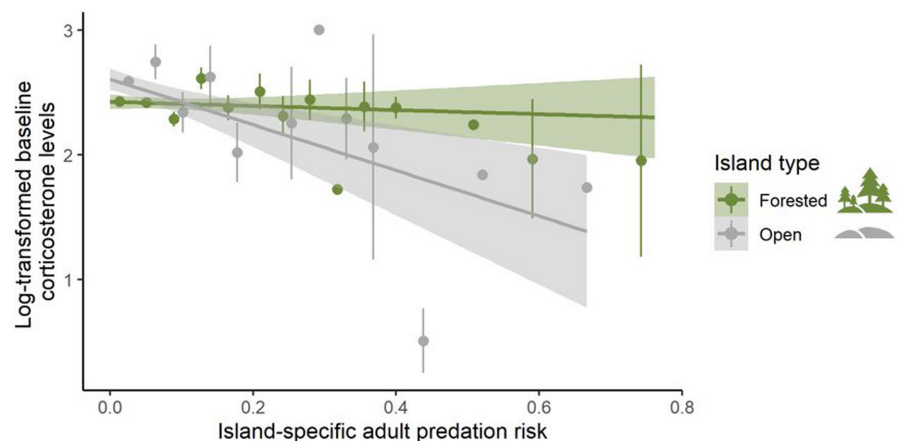
in baseline CORT levels with respect to most of the investigated factors, by highlighting significant but relatively low CORT repeatability ($R \pm SE = 0.19 \pm 0.03$) as well as plastic responses to variation in extrinsic (predation risk indices) and intrinsic (clutch size and age) conditions.

## 4.1 | CORT and reproductive investment: Support for the CORT-adaptation hypothesis

Baseline CORT levels were higher in intermediate-aged and early breeding females and in those laying larger clutches. Higher baseline CORT levels were also associated with better hatching success. Altogether, these results favour the CORT-adaptation hypothesis over the CORT-fitness hypothesis, as the former postulates a positive association between baseline glucocorticoid levels and fitness (Bonier et al., 2009).

In line with the CORT-adaptation hypothesis, females displayed higher baseline CORT levels when incubating larger clutches (within-individual effect). This result is robust to excluding the smallest and largest clutches (indicating potential partial clutch predation and conspecific brood parasitism, respectively; Figure 3). Noteworthy, our study is among the first ones to provide evidence for within-individual plasticity in the relationship between CORT and clutch size in a wild animal population (but see Love et al., 2008). Because clutch size is tightly associated with the reproductive value of the clutch (Hanssen et al., 2022), this finding supports a functional link between CORT and reproductive investment. Indeed, increased baseline CORT levels have previously been associated with higher incubation commitment (Ouyang et al., 2013) and nestling quality (Bonier et al., 2011; Rivers et al., 2017). Elevated CORT levels may also reflect the higher allostatic load (Tinbergen & Williams, 2002; Williams, 1996) or metabolic cost (Jimeno et al., 2020) of incubating a larger clutch and maintaining an optimal incubation temperature for the eggs (Erikstad & Tveraa, 1995). Yet, despite its important role in the mobilisation of stored energy reserves (Harris, 2020; Landys et al., 2006; Sapolsky et al., 2000), we did not detect any association between female baseline CORT and body condition, a proxy of energy reserves. A likely explanation is that no female had reached phase III of fasting, a critical phase associated with protein catabolism and elevated CORT levels (Cherel et al., 1988).

In further support of the CORT-adaptation hypothesis and paralleling previous findings (Angelier et al., 2006; Carlitz et al., 2022), baseline CORT levels plastically increased with female age, before decreasing in the oldest breeders (within-individual effect). Given our results on clutch size and hatching success, this suggests that CORT mediates an increase in reproductive investment with age and physiological senescence at old age. Accordingly, there is ample experimental and theoretical evidence that reproductive performance increases with age and experience before declining at very old ages (e.g. in eiders; Mohring et al., 2022; Noreikienė et al., 2021). To our knowledge, our study provides the first evidence of a within-individual decrease in baseline CORT levels at old age (but see

Lendvai et al. (2015) for an individual-specific decrease in the CORT stress response with age), supporting the idea that CORT can mirror reproductive senescence in wild animals.

We found that females with higher baseline CORT also had better hatching success (among-individual effect), further supporting a positive link between CORT and reproductive investment, as predicted by the CORT-adaptation hypothesis. Interestingly, however, we did not detect any effect of within-individual variation in baseline CORT levels on hatching success. This suggests that CORT levels may reflect among-individual variation in individual quality, as some females consistently perform better than others in eiders (Öst & Steele, 2010). In line with this idea, we found that early breeders displayed higher baseline CORT levels in our study population. In many wild vertebrates including eiders, higher-quality females indeed breed earlier or have a higher reproductive investment (Descamps et al., 2011; Goutte, Angelier, Chastel, et al., 2010; Verhulst & Nilsson, 2008).

## 4.2 | Plasticity in the CORT response to predation threat

Previous studies have highlighted an association between the chronic stress induced by predator presence and sustained elevation of baseline glucocorticoid levels (Dulude-de Broin et al., 2020; Newman et al., 2013; Scheuerlein et al., 2001; Spong et al., 2020), especially in contexts where elevated baseline CORT has negative impacts on fitness. Here, we instead showed that increasing predation pressure was correlated with a decrease in baseline CORT levels. Furthermore, breeding during years of high predator abundance or under higher island-specific adult predation risk was associated with an individually plastic decrease in female baseline CORT levels, although this latter effect was only evident on open islands. Besides predation risk, female body condition at hatching has concurrently increased in this population (Mohring et al., 2022; Öst et al., 2022), but the fact that body condition was unrelated to baseline CORT levels (this study) makes confounding by temporal trends in body condition unlikely. Food availability is another potential confounding factor, as it may affect allostatic load and hence baseline CORT levels (reviewed in Busch & Hayward, 2009). However, the study area has maintained abundant and stable populations of blue mussels *Mytilus trossulus*—the main prey of eiders—throughout the study period (Jaatinen et al., 2021). As baseline CORT is also positively associated with reproductive investment and hatching success in the study system (see 4.1), our results therefore suggest that a decrease in reproductive investment is associated with increased predation pressure (Ghalambor & Martin, 2000). This conclusion is further supported by a significant reduction of clutch size over the study period (Mohring et al., 2022), which is consistent with previous experimental work showing that clutch size and reproductive investment are reduced under higher predation risk (Doligez & Clobert, 2003; Zanette et al., 2011). Intriguingly, these decreases

in reproductive investment and baseline CORT were not associated with a population-level decrease in hatching success. Concomitant population-level changes may prevent the detection of a temporal trend in hatching success. For example, white-tailed eagle recovery has been associated with a change in the breeding habitat of eiders that now nest under thicker vegetation cover (Mohring et al., 2022) where clutch depredation is lower (Öst et al., 2008, 2018).

Nesting under higher adult predation risk was associated with a plastic reduction of female baseline CORT levels. What makes this finding particularly interesting is that this plasticity was habitat-specific, only being evident on open islands. Open islands provide little visual concealment from predators, and have been associated with lower survival rates of breeding females (Ekroos et al., 2012; Öst et al., 2018). Such habitats may favour an adaptive shift in allocation strategy from reproductive investment to adult survival and consequent nest desertion, mediated by decreased baseline CORT levels (Wingfield & Sapolsky, 2003). On forested islands, increased concealment may allow females to maintain high maternal investment irrespective of surrounding predation risk, mediated by elevated CORT levels as postulated by the CORT-adaptation hypothesis. In addition, it is noteworthy that we did not find a relationship between baseline CORT levels and nest predation risk. As long-lived birds, female eiders are expected to prioritise their own survival at the expense of their current reproductive event (Ghalambor & Martin, 2001; Williams, 1966), resulting in stronger behavioural and physiological responses to adult predation risk. In line with this, adult predation risk, rather than nest predation risk, was associated with plastic adjustments of escape behaviour in eiders (Mohring et al., 2022).

## 5 | CONCLUSIONS

Using long-term individual-based data, we showed that increasing predation pressure was associated with both a reduction in baseline CORT and a concomitant decrease in reproductive investment. Importantly, our study provides strong support for the CORT-adaptation hypothesis as we found that all our direct and indirect proxies of reproductive investment were positively associated with baseline CORT levels. Our study shows that changes in predation regime are not only associated with population-level changes in reproductive investment, but also with plastic adjustment of individual endocrine responses under severe predation pressure. Thus, baseline CORT levels, showing only weak repeatability, demonstrate considerable phenotypic plasticity. Indeed, individuals showed adjustments in baseline CORT levels consistent with changes in predation risk, displaying lower CORT levels when nesting in years of high eagle abundance or on open, unsheltered islands characterised by higher adult predation risk. Importantly, despite the drastic change in predation regime, the correlational nature of this study does not allow to draw conclusions on the mechanistic link between baseline CORT levels and predation pressure.

In the current context of climate change, other unmonitored environmental variables may have concomitantly fluctuated over the study period and affected baseline CORT levels. Such variables may for instance include changes in ambient temperature (De Bruijn & Romero, 2018; Hau et al., 2022; Mentesana & Hau, 2022; Ruuskanen et al., 2021) or bottom-up effects linked to variation in food quality or availability (Kitaysky et al., 2010). In light of our results, we urge future studies to experimentally test for a causal relationship between predation pressure and baseline CORT levels, while controlling for other potential important environmental variables.

## AUTHOR CONTRIBUTIONS

Bertille Mohring, Frédéric Angelier, Markus Öst and Kim Jaatinen conceived the ideas and designed methodology. Bertille Mohring, Markus Öst and Kim Jaatinen collected the data. Charline Parenteau, Emmanuelle Grimaud, Bertille Mohring and Frédéric Angelier conducted laboratory analyses. Bertille Mohring analysed and interpreted the data with contributions from Frédéric Angelier, Markus Öst and Kim Jaatinen. Bertille Mohring led the writing of the manuscript and Frédéric Angelier, Markus Öst, Kim Jaatinen, Charline Parenteau and Emmanuelle Grimaud contributed to writing the article. All authors contributed critically to the drafts and gave final approval for publication.

## CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xd2547dpj.

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## SUPPORTING INFORMATION

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

**Supplementary Material S1.** Temporal variation in the average daily number of white-tailed eagle sightings between April 1 and June 15 (a period corresponding to eider breeding season in Southern Finland) between 1990 and 2022. White-tailed eagle abundance monitoring is carried out at Hanko Bird Observatory (HALIAS, 59°49′ N, 22°54′ E), located ca 20 km from the study area. The dashed vertical line presents the start of the monitoring of eider baseline corticosterone levels (2009).

**Supplementary Material S2.** Numbers of baseline corticosterone samples, unique female common eider sampled and mean ± standard deviation (SD) number of replicates per individual on open and forested islands.

**Supplementary Material S3.** Description of corticosterone radioimmunoassay.

**Supplementary Material S4.** Linear mixed models (LMMs) within ΔAICc ≤2 explaining variation in female common eider baseline corticosterone levels in relation to intrinsic (clutch size 'CS', female maternal experience and its quadratic effect, body condition 'BC', relative laying date 'RLD') and extrinsic variables (eagle index, island-specific adult and nest predation risk 'ad pred' and 'nest pred', island type, and the interactions between island type and island-specific adult predation risk and eagle index, respectively). The most parsimonious model and significant effects ($p ≤ 0.05$) are presented in bold.

**Supplementary Material S5.** Model-averaged coefficient estimates (E), standard errors (SE), z-values (z) and p-values (p) derived from the top-ranked linear mixed models (LMMs) within ΔAICc ≤2 explaining

variation in female common eider baseline corticosterone levels in relation to intrinsic (clutch size, female maternal experience and its quadratic effect, body condition, relative laying date) and extrinsic variables (eagle index, island-specific adult and nest predation risk, island type, and the interactions between island type and island-specific predation risk indices and eagle index, respectively). Significant effects ($p \leq 0.05$) are presented in bold.

**Supplementary Material S6.** Linear mixed models (LMMs) explaining variation in baseline corticosterone levels in relation to within- and among-individual changes in quantitative explanatory variables. The significance of within- and among-individual effects was tested following (eq. 2) in van de Pol and Wright (2009) and the difference between within- and among-individual slopes was tested following (eq. 3) in van de Pol and Wright (2009). Significant $p$-values ($p \leq 0.05$) for (eq. 2) indicate that the within-individual or among-individual slope is different from zero. Non-significant $p$-values for (eq. 3) indicate that within- and among-individual slopes are not distinguishable (i.e., that within-individual variation in the focal variable explains the variation in baseline corticosterone levels). Only independent variables for which both within- and among-individual effects were significant are presented, and each focal variable was tested in a separate model, with all other variables included as covariates and female identity and year as random effects. Significant effects are presented in bold.

**Supplementary Material S7.** Relationship between female common eider log-transformed baseline corticosterone levels and clutch size (i.e., number of eggs in the clutch). The population-level regression line is presented in black, with grey areas accounting for 95% confidence intervals. Grey lines represent individual-level responses to clutch size variation (raw slopes fitted for each female, not model predictions).