



Parental Investment Under Predation Threat in Incubating Common Eiders (*Somateria mollissima*): A Hormonal Perspective

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Predation risk affects the costs and benefits of prey life-history decisions. Predation threat is often higher during reproduction, especially in conspicuous colonial breeders. Therefore, predation risk may increase the survival cost of breeding, and reduce parental investment. The impact of predation risk on avian parental investment decisions may be hormonally mediated by prolactin and corticosterone, making them ideal tools for studying the trade-offs involved. Prolactin is thought to promote parental care and commitment in birds. Corticosterone is involved in allostasis and may either mediate reduced parental investment (corticosterone-fitness hypothesis), or promote parental investment through a reallocation of resources (corticosterone-adaptation hypothesis). Here, we used these hormonal proxies of incubation commitment to examine the impact of predation risk on reproduction in common eiders (*Somateria mollissima*) breeding in the Baltic Sea. This eider population is subject to high but spatially and temporally variable predation pressure on adults (mainly by the white-tailed eagle *Haliaeetus albicilla* and introduced mammalian predators) and nests (by the adult predators and exclusive egg predators such as hooded crows *Corvus cornix*). We investigated baseline hormonal levels and hatching success as a function of individual quality attributes (breeding experience, female and duckling body condition), reproductive investment (clutch weight), and predation risk. We expected individuals nesting in riskier environments (i.e., on islands where predation on adults or nests is higher, or in less concealed nests) to reduce their parental investment in incubation, reflected in lower baseline prolactin levels and either higher (corticosterone-fitness hypothesis) or lower (corticosterone-adaptation hypothesis) baseline corticosterone levels. Contrary to our predictions, prolactin levels showed a positive correlation with nest predation risk. The unexpected positive relationship could result from the selective disappearance of low-quality females (presumably having low prolactin levels) from risky sites. Supporting this notion, female body condition and hatching success were positively correlated with predation risk on females, and baseline prolactin concentrations were positively correlated with duckling body condition, a proxy of maternal quality. In line with the

corticosterone-adaptation hypothesis, baseline corticosterone levels increased with reproductive investment, and were negatively associated with nest predation risk. Hatching success was lower on islands where nest predation risk was higher, consistent with the idea of reduced reproductive investment under increased threat. Long-term individual-based studies are now needed to distinguish selection processes occurring at the population scale from individually plastic parental investment in relation to individual quality and variable predation risk.

Keywords: corticosterone, prolactin, individual quality, parental care, predation risk, reproductive success, common eider (*Somateria mollissima*)

INTRODUCTION

Predation exerts both direct and indirect effects on prey, and these effects show considerable spatiotemporal variation (Lima, 1998; Laundré et al., 2010). Whereas predators affect prey populations by direct killing, their mere presence also induces behavioral and physiological changes in prey (Lima, 1998). Such changes include increased aggregation tendency (Lehtonen and Jaatinen, 2016), altered habitat use (Turner, 1996; Creel et al., 2005), increased sensitivity to disturbance (Gómez-Serrano, 2020), and altered activity budgets (Pöysä, 1987; Blumstein and Daniel, 2005; Öst and Tieraal, 2011). During the breeding season, the presence of predators affects the costs and benefits of parental investment, often leading to an exacerbated “cost of reproduction” (Slagsvold, 1984; Magnhagen, 1991). Indeed, reproducing prey are particularly exposed to predation by the risky behaviors they adopt to find a partner, mate, and successfully raise their offspring (Thomas, 1988; Magnhagen, 1991; Arnold et al., 2012). Consequently, decreased investment in current reproduction is expected under elevated predation risk, a prediction verified in birds laying smaller clutches when exposed to high risk (Doligez and Clobert, 2003; Eggers et al., 2006; Zanette et al., 2011; Noreikiene et al., 2021).

Reproduction is a costly life-history event not only because of its effect on survival (Magnhagen, 1991; Schwarzkopf and Shine, 1992; Arnold et al., 2012), but also because of elevated energy expenditure (Krapu, 1981). Life-history theory thus predicts a trade-off between individual investment in reproduction and survival (Williams, 1966). The cost of reproduction varies depending on individual state and quality (Feifarek et al., 1983; Reznick, 1985; Hamel et al., 2009), but also prevailing environmental conditions (De Steven, 1980; Reznick, 1985). In long-lived species, current parental investment is generally expected to be higher under favorable environmental conditions and individual states, i.e., when resources are plentiful (Whittingham and Robertson, 1994; Storey et al., 2017), weather conditions are benign (Thierry et al., 2013), predation risk is low (Ghalambor and Martin, 2000), and when individuals are in good condition (Chastel et al., 1995; Tveraa et al., 1998). On top of these factors, long-lived species should invest more into current reproduction as the prospects of future reproduction diminish with advancing age (the restraint hypothesis, Curio, 1983; Heidinger et al., 2006), even if environmental conditions are far from being optimal. This prediction has been well

supported empirically (Forslund and Pärt, 1995; Prévault et al., 2005; Angelier et al., 2007a,b). As a consequence of this survival-reproduction trade-off, individuals are predicted to modulate their allocation to current reproduction (Reznick, 1985), and may even completely refrain from current reproduction by skipping breeding under prohibitively high costs of reproduction (Chastel et al., 1995; Erikstad et al., 1998; Bruinzeel, 2007; Öst et al., 2018).

Hormonal mechanisms are involved in the mediation of life-history decisions when coping with a range of stressors including predation risk (Ricklefs and Wikelski, 2002). In birds, prolactin and corticosterone are especially relevant to study parental investment. Prolactin is the main hormone involved in the expression of parental behavior, and prolactin levels can be a reliable proxy of parental investment and reproductive involvement (Angelier and Chastel, 2009; Angelier et al., 2016; Smiley, 2019). Consequently, circulating blood prolactin concentrations are elevated during reproduction (Crisuolo et al., 2002; Vleck and Vleck, 2011). Furthermore, individuals with higher prolactin levels may provide better parental care (Angelier and Chastel, 2009; Smiley and Adkins-Regan, 2016, 2018), such as higher brood provisioning (Miller et al., 2009; Smiley and Adkins-Regan, 2016, 2018) and incubation commitment (Angelier et al., 2015; Wang et al., 2020), or even shorter latency to return to the nest after a disturbance (Angelier et al., 2009; Hope et al., 2020). Importantly, circulating prolactin levels have been shown to decrease in response to stressor, poor body condition, or low food availability (Delehanty et al., 1997; Groscolas et al., 2008; Angelier and Chastel, 2009; Riechert et al., 2014a). This is associated with a concomitant reduction of parental care, suggesting that prolactin may mediate parental responses to environmental conditions (Angelier et al., 2016).

Corticosterone, on the other hand, is involved in the maintenance of homeostasis (McEwen and Wingfield, 2003; Romero et al., 2009) and in the response to environmental challenges (Angelier and Wingfield, 2013; Wingfield, 2013). The corticosterone-fitness hypothesis states that circulating corticosterone levels are negatively associated with performance and fitness, because elevated baseline corticosterone levels may reflect higher energetic demand induced by deteriorating environmental conditions (Wingfield et al., 1983; Kitaysky et al., 2007), and may be associated with reduced survival and breeding success (Silverin, 1986; Angelier et al., 2010; Goutte et al., 2010; Vitousek et al., 2018; Breuner and Berk, 2019). For example, high circulating corticosterone levels have been shown

to be involved in a reduction of parental care (Silverin, 1986; Angelier et al., 2009; Ouyang et al., 2011; Lynn, 2016; Schoenle et al., 2017), or even induce nest abandonment (Wingfield et al., 1983; Robin et al., 1998; Groscolas and Robin, 2001; Spée et al., 2011). In contrast, circulating corticosterone levels may also be positively associated with fitness, as stated by the corticosterone-adaptation hypothesis (Bonier et al., 2009). Indeed, elevated baseline corticosterone levels may enhance energy mobilization (Romero, 2002; Breuner, 2011) and therefore promote reproductive effort (Riechert et al., 2014a). For example, elevated baseline corticosterone levels have been associated with higher incubation effort (Ouyang et al., 2013), higher brood provisioning (Miller et al., 2009; Bonier et al., 2011; Ouyang et al., 2013), or higher offspring production (Bonier et al., 2011; Love et al., 2014). Importantly, the association between fitness and corticosterone may be dose-dependent (Bonier et al., 2009). In line with hormetic mechanisms (Costantini et al., 2010; Costantini, 2014), the corticosterone-fitness hypothesis may be validated under high levels of baseline corticosterone, while the corticosterone-adaptation hypothesis may be validated under lower baseline corticosterone levels.

Here, we investigate to what extent prolactin and corticosterone—two endocrine mediators of parental investment—are affected by predation risk in a long-lived ground-nesting bird, the common eider (*Somateria mollissima*), hereafter eider. Specifically, baseline prolactin and corticosterone levels have been shown to be closely related to incubation commitment in several species (Ouyang et al., 2013; Schoenle et al., 2017; Bowers et al., 2019; Hope et al., 2020), including the eider (Crisuolo et al., 2002, 2005). We therefore expect female eiders, as a long-lived species, to display lower baseline prolactin levels and either higher (corticosterone-fitness hypothesis) or lower (corticosterone-adaptation hypothesis) baseline corticosterone levels at the end of incubation if they reduce their investment in incubation as a response to increased predation threat. In our study area in SW Finland, northern Baltic Sea, female eiders nest on islands showing substantial spatial and temporal variation in predation pressure on adults and their nests (Öst et al., 2018) as well as in nest concealment (Öst and Steele, 2010), allowing us to test the impact of predation risk on variation in these endocrine traits and hatching success. We analyzed baseline hormone levels (prolactin and corticosterone) as a function of direct or indirect proxies of female quality (i.e., breeding experience, female body condition, offspring body condition), energetic investment in current reproduction (clutch weight), and predation risk on incubating female eiders and nests. In addition, we examined the endocrine correlates of reproductive success (i.e., hatching success). We expect (1) higher baseline prolactin and either lower (corticosterone-fitness hypothesis) or higher (corticosterone-adaptation hypothesis) baseline corticosterone levels in high-quality breeders and/or birds producing heavier clutches, as experience and condition are known to influence hormone levels (Angelier et al., 2007b; Bókony et al., 2009; Breuner, 2011). We also expect (2) birds nesting in riskier environments (i.e., on islands where predation on adults or nests is higher, or in less concealed nests) to have lower prolactin levels and either higher (corticosterone-fitness

hypothesis) or lower (corticosterone-adaptation hypothesis) corticosterone levels, reflecting lower investment in incubation under increased threat. Finally, due to the link between parental investment and both prolactin and corticosterone levels (Angelier and Chastel, 2009; Bonier et al., 2009), we expect (3) lower baseline prolactin levels and either higher (corticosterone-fitness hypothesis) or lower (corticosterone-adaptation hypothesis) baseline corticosterone levels to be associated with poorer reproductive performance (i.e., reduced hatching success).

MATERIALS AND METHODS

Study Area and Species

Study Area and Female Monitoring

Fieldwork was conducted in the archipelago surrounding Tvärminne Zoological Station (59°50'N, 23°15'E), in the western Gulf of Finland, in 2013. In this area, female eiders nest on islands of various sizes ($N = 17$ islands, mean area \pm SD = 1.78 ± 2.72 ha, min = 0.13 ha, max = 10.22 ha). Vegetation cover varies from bare rocks and sparse patches of herbs or stands of juniper (*Juniperus communis*) to pine (*Pinus sylvestris*) dominated forest. The study islands are relatively close to each other, typically only hundreds of meters apart, in a total study area of ca 15 km². Nevertheless, islands vary considerably in predation risk on both incubating females and their nests (Öst et al., 2011), due to variable forest cover (Ekroos et al., 2012; Öst et al., 2018) and range of available nest micro-habitats in terms of concealment (Seltmann et al., 2014). Importantly, the breeding period represents a period of elevated predator-induced mortality in this ground-nesting bird, and thus the survival of adult females is lower than that of males in eider populations subject to significant predation risk (Ramula et al., 2018).

Eiders are long-lived ground-nesting birds, with a mean life expectancy of ca. 21 years (Coulson, 1984). The eider breeding population at Tvärminne has been monitored every year since 1990. Incubating female eiders were trapped on their nest with hand nets between May and early June to measure hormone levels ($N = 148$ out of 355 breeding females in 2013). Females incubate for about 26 days (Korschgen, 1977), and incubating birds were captured predominantly during the later phase of incubation to minimize nest abandonment (mean \pm SD = 17.6 ± 4.6 days after the start of incubation, range = 6.5–25.5 days). Incubation stage was estimated using an egg floatation test (Kilpi and Lindström, 1997). Each trapped female was ringed with a standard metal ring and a unique color-ring combination, weighed to the nearest 5 g with a Pesola spring balance, and its radius-ulna length was measured to the nearest 1 mm with a wing ruler as a proxy of body size.

Breeding Experience, Body Condition, and Clutch Weight

We characterized female breeding experience using a qualitative indicator (Jaatinen and Öst, 2011). We categorized females as either experienced (already ringed when captured) or inexperienced breeders (unringed at capture; only adult breeders

are ringed in the study area). As eiders are philopatric (Swennen, 1990, 1991; Coulson, 2016) and show high nest-site fidelity (Öst et al., 2011; Coulson, 2016), and as the majority of breeding females are captured annually (trapping success in 2013 = 65.1%), with a constant trapping effort since 1996 (Jaatinen and Öst, 2011), this indicator of breeding experience can be considered reliable.

For each trapped female, we calculated two indices of body condition: one measured when the bird was trapped and sampled for blood (physiological parameters are expected to vary according to the instantaneous condition at the time of sampling, Kitaysky et al., 1999; Riechert et al., 2014b), and the other estimated at hatching (to allow direct comparison between females by taking into account weight loss during incubation, see below). To avoid any weight bias due to females potentially still laying eggs, only females that had incubated for more than 5 days were kept for further analyses. Body condition at trapping was calculated as the standardized residuals of a linear regression of log-transformed weight on log-transformed radius-ulna length. As eiders fast and lose weight during incubation (Crisuolo et al., 2000), it is essential to take into account the incubation stage to compare individual differences in energy reserves, in addition to structural size. Hence, we estimated body condition at hatching. To do so, we used the standardized residuals of a linear regression of log-transformed estimated weight at hatching on log-transformed radius-ulna length (Öst et al., 2008). Weight at hatching was estimated as the weight of the female at trapping subtracted by the estimated weight that the female was expected to lose during the remaining incubation time (estimated log-transformed daily weight loss: $E \pm SE = -0.221 \pm 0.004$, $t = -51.64$, $P < 0.001$). This estimate of mean weight loss rate during incubation was derived as the slope of the linear regression of log-transformed body mass on log-transformed incubation time and projected hatching date (see Öst and Steele, 2010). In addition, for each trapped female, total clutch weight was measured to the nearest 1 g in order to control for a potential influence of clutch weight on endocrine traits. Because eggs lose mass during development, we corrected clutch mass for incubation stage, evaluated by egg floatation, by extracting the residuals obtained from the linear regression of clutch weight on incubation stage.

Endocrine Correlates of Parental Investment

In 2013, a total of 148 breeding female eiders were trapped on the nest and sampled for blood (~1.5 mL) from the ulnar vein within 3 min following capture (mean \pm SD = 2.42 \pm 0.35 min, range = 1.67–3.22 min) in order to obtain baseline hormonal levels (Romero and Reed, 2005). Baseline corticosterone levels were not related to sampling time (linear regression: $t = 1.23$, $P = 0.22$, $r^2 = 0.004$); hence the two blood samples taken after 3 min (3.12 and 3.22 min) were kept for further analyses. Blood samples were centrifuged and plasma was stored at -20°C until assay. Plasma concentrations of corticosterone and prolactin were determined by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé (CEBC), as previously described (corticosterone: Lormée et al., 2003; Öst et al., 2020); prolactin: Criscuolo et al., 2002) (corticosterone, 5 assays, inter-assay CV:

14.31%, intra-assay CV: 10.97%; prolactin, 2 assays, inter-assay CV: 12.05%, intra-assay CV: 11.32%).

Hatching Success and Offspring Condition

For each nest, hatching success (0: failure, 1: success) was determined by returning to the nest at the end of incubation and monitoring the presence of ducklings. The eider is a precocial species and ducklings usually leave the nest within 24 h of hatching (Öst and Bäck, 2003). If no ducklings were found in the nest, they had either already hatched and left the nest, or the nest had been depredated. Consequently, egg shells were examined to determine if the breeding attempt had been successful or not. Hatched eggs were recognizable by their intact leathery membrane while depredated nests had either no eggs or eggs broken into pieces, usually with a bloody membrane still attached to the shells (Bolduc et al., 2005; Öst and Steele, 2010). A nest was considered as hatched if at least one duckling or one hatched egg membrane was found.

If ducklings ($N = 209$) were found in the nest ($N = 66$ out of 93 successful nests), their tarsus length was measured to the nearest 0.1 mm with a Vernier caliper and they were weighed to the nearest 1 g. Duckling body condition was estimated as a proxy of offspring quality by extracting the standardized residuals of the linear regression of log-transformed body weight against log-transformed tarsus length (Öst et al., 2020).

Assessment of Predation Risk

Nest-Site Micro-Habitat

Females breed on the ground under variable cover and mainly rely on crypsis to avoid being detected by predators. Concealment mainly offers protection from avian predators, and to a lesser extent from mammalian predators. To quantify nest concealment, we measured the amount of nest cover (including all layers of vegetation from ground level to canopy, including rocks) above each nest based on hemispherical photographs. To do so, we used a 42-mm fisheye lens mounted on an Olympus C-740 digital camera placed in each nest cup and aimed vertically (Öst and Steele, 2010; Jaatinen et al., 2014). Each picture was converted to black and white and the proportion of black pixels (corresponding to vegetation or other obstacles, e.g., rocks) was measured using Image Tool (version 3.00; University of Texas Health Science Center, San Antonio).

Island-Specific Female and Nest Predation Risk

Breeding females and their eggs are subject to predation from native and non-native species. The main predators of incubating females are the native white-tailed eagle (*Haliaeetus albicilla*), the population of which has increased rapidly since the 1990s (Stjernberg et al., 2005; Öst et al., 2018), the eagle owl (*Bubo bubo*) as well as two introduced mammals: the American mink (*Neovison vison*) and the raccoon dog (*Nyctereutes procyonoides*) (Jaatinen and Öst, 2013; Öst et al., 2018). In addition, eggs are depredated either by primary predators of female eiders, or by nest predators such as hooded crows (*Corvus cornix*) or gulls (*Larus* spp.) (Jaatinen et al., 2014). The latter consume eggs either when the female is absent from the nest or act as secondary predators after the female has been attacked on the nest.

In order to distinguish between these different types of predation, we determined for each island an index of adult female and nest predation risk, respectively. These two indices are based on confirmed cases of depredated females or nests rather than unsuccessful predation attempts, as the latter are impossible to document in the field without camera surveillance. However, one should expect a close correlation between the incidence of successful and unsuccessful predation attempts. Female predation risk was calculated as the island-specific proportion of killed nesting females (number of killed females divided by the number of breeding attempts). Island-specific nest predation risk was calculated based on hatching success information (see above). The number of successful (i.e., hatched) nests at the final nest fate census was divided by the number of nests on the island for whose fate (success or failure) was known (326 known nest fates out of 355 monitored nests; 91.8% of known nest fates; mean number of nests per island \pm SD = 31 ± 17 nests). The main reason for nest failure was depredation (136 out of the 155 failed nests; 87.7%) and the low number of non-depredated but failed nests could be explained by females incubating infertile or unviable eggs. Thus, island-specific nest predation was calculated as: 1-island-specific proportion of successful nests. Both island-specific female and nest predation risk varied considerably between islands (female predation risk: mean \pm SD = 0.03 ± 0.04 , min = 0.00, max = 0.10; nest predation risk: mean \pm SD = 0.42 ± 0.20 , min = 0.00, max = 0.86, $N = 17$ islands).

Statistical Analyses

All statistical analyses were conducted in R 3.6.1. (R Core Team, 2018). We used linear mixed models (LMMs) (R function “lme,” nlme package; Pinheiro et al., 2019) and generalized linear mixed models (GLMMs) (R function “glmer,” lme4 package; Bates et al., 2015) to investigate variation in baseline prolactin and corticosterone levels, reproductive success and duckling body condition, in relation to the aforementioned individual and environmental explanatory variables. We checked that all models met the assumptions of normality and homoscedasticity of residuals. Consequently, baseline corticosterone levels were log-transformed as $\ln(x + 1)$ to meet model assumptions. Model selection was performed using a stepwise backward elimination method in which non-significant terms ($P > 0.05$) were eliminated at each step. We preferred a stepwise model selection approach due to its ease of interpretation and presentation, but acknowledge its potential limitations (Smith, 2018). To verify the robustness of our model selection procedure, we therefore also performed conditional model averaging across best-ranked models (Δ AICc < 2) for the dependent variables, using the function “dredge” in the R-package MuMIn (Barton, 2020). This robustness check confirmed that we had correctly identified the final models and significance of each included explanatory variable for nearly all analyses in this paper. The only exception was the analysis of female body condition at hatching; here, the association with adult predation risk was only a trend when performing model averaging (see Results below). For each model, we relied on the variance inflation factor (VIF) to look for multicollinearity among candidate variables. We did not detect

any multicollinearity among the candidate variables of selected models (all VIF < 2.5 ; Allison, 2012).

Physiological Responses

To study the variation in female physiology in relation to proxies of individual quality, maternal investment and predation risk, we constructed two sets of LMMs, where baseline prolactin and corticosterone levels were included as the dependent variable, respectively. The explanatory individual state variables were body condition at trapping, breeding experience, incubation stage, radius-ulna length, and incubation-stage corrected clutch weight. Baseline corticosterone was also included in the models investigating baseline prolactin variation to assess the potential effect of corticosterone on prolactin levels (Angelier and Chastel, 2009; Angelier et al., 2009; Vleck and Vleck, 2011). Furthermore, the following predation risk related explanatory variables were included in the models: nest cover, nest predation risk and female predation risk. One extremely high baseline prolactin value (value = 343.82 ng/mL, mean \pm SD = 149.56 ± 43.81 ng/mL, min = 57.56 ng/mL, max = 343.82 ng/mL) was removed from statistical analyses. To account for the potential non-independence of physiological responses of individuals breeding on the same island, island identity was added to all models as a random effect.

Hatching Success and Duckling Quality

As reproductive success followed a binomial distribution (0: failure, 1: success), we built GLMMs with a binomial error distribution, with reproductive success as the dependent variable and baseline prolactin and corticosterone levels, individual characteristics (body condition at hatching, breeding experience, radius-ulna length, and clutch weight) and environmental factors (nest cover, island-specific nest and female predation risk) as explanatory variables. As the probability of a nest being depredated is likely to decrease as it gets closer to hatching (due to a shorter time left for the predator to detect the nest), we also included incubation stage (i.e., the number of days since egg laying) as an explanatory variable. Island identity was included as a random effect to account for the potential pseudoreplication arising from repeated observations from each island.

We used LMMs to study the association between female baseline prolactin and corticosterone levels (explanatory variables) and duckling body condition (dependent variable), a proxy of offspring quality. As ducklings belonging to the same clutch are not independent from each other, and as we expect non-independence between the body conditions of ducklings hatching on the same islands, clutch and island identity were added as random effects in these models.

Body Condition at Hatching

Covariation between individual quality and reproductive success may influence the observed relationship between maternal hormone profiles and parental investment, e.g., if early breeding failure disproportionately affects poor-quality individuals. To assess whether such selective disappearance may occur, we analyzed variation in female body condition, a proxy of female quality, in relation to female attributes and predation risk.

In these LMMs, female body condition at hatching was the dependent variable and breeding experience, nest predation risk and female predation risk were explanatory variables. Island identity was included as a random effect to account for the non-independence of body conditions of females nesting on the same island.

RESULTS

Baseline Prolactin in Relation to Individual and Environmental Characteristics

The final model explaining variation in baseline prolactin levels only included nest predation risk (Table 1). Thus, baseline prolactin levels showed a significant positive association with increasing nest predation risk (nest predation risk effect, parameter estimate \pm standard error: $E \pm SE = 45.41 \pm 21.24$; Table 1 and Figure 1A), but showed no significant association with female predation risk. Likewise, the final model explaining variation in baseline prolactin did not show a significant association between baseline prolactin levels and breeding experience, structural size, condition at trapping, clutch weight, or nest cover.

Baseline Corticosterone in Relation to Individual and Environmental Characteristics

The final model explaining variation in baseline corticosterone levels included breeding experience, clutch weight and nest predation risk (Table 1). Baseline corticosterone levels were significantly higher in experienced birds compared to first-time breeders (baseline corticosterone concentration: inexperienced females: mean \pm SE = 9.87 ± 0.71 ng/mL; experienced females: mean \pm SE = 17.06 ± 1.25 ; Table 1 and Figure 2). Baseline corticosterone also showed a significantly positive relationship with clutch weight ($E \pm SE = 0.0013 \pm 0.0005$; Table 1 and

Figure 2). In contrast, female structural size, body condition or nest cover were not related to baseline corticosterone concentrations. With respect to our predation indices, increasing island-specific nest predation risk had a significant negative association with corticosterone levels ($E \pm SE = -0.97 \pm 0.39$; Table 1 and Figure 1B), whereas female predation risk did not explain variation in baseline corticosterone levels.

Hatching Success in Relation to Physiology, Individual and Environmental Characteristics

The final model predicting hatching success included baseline prolactin, radius-ulna length, and female and nest predation risk, as explanatory variables (Table 1). Hatching success showed a significant negative relationship with increasing baseline prolactin levels ($E \pm SE = -0.012 \pm 0.005$; Table 1 and Figure 3A), while it did not significantly vary with baseline corticosterone levels (Figure 3B). Hatching success tended to increase with female structural size, although this effect was not significant (Table 1). Other individual explanatory variables (incubation stage, body condition at hatching and breeding experience) were not selected in the final model. We also did not find any significant association between nest cover and hatching success. However, we also found that hatching success was significantly negatively related to nest predation risk ($E \pm SE = -8.85 \pm 2.46$; Table 1 and Figure 3C) and significantly positively associated with female predation risk ($E \pm SE = 14.18 \pm 6.86$; Table 1 and Figure 3D).

Female Body Condition in Relation to Individual Attributes and Predation

Female body condition at hatching was related to individual and environmental factors (Table 1). Body condition at hatching was significantly higher in more experienced birds (body condition at hatching: inexperienced females: mean \pm SE = 0.16 ± 0.08 ; experienced females: mean \pm SE = 0.62 ± 0.08 ; Table 1 and Figure 4). Body condition at hatching also showed a significant positive correlation with female predation risk ($E \pm SE = 4.03 \pm 1.90$; Table 1 and Figure 4), although this association was only marginally significant ($E \pm SE = 0.15 \pm 0.08$; $Z = 1.756$, $P = 0.079$) when performing conditional model averaging. In addition, female body condition at hatching was not significantly related to nest predation risk.

Offspring Body Condition and Maternal Hormone Profiles

Duckling body condition was significantly positively associated with maternal baseline prolactin concentrations ($E \pm SE = 0.006 \pm 0.003$; $\chi^2 = 4.481$, $P = 0.034$; Figure 5A), but showed no association with maternal baseline corticosterone levels ($\chi^2 = 4.481$, $P = 0.907$; Figure 5B).

TABLE 1 | Final LMMs and GLMM explaining baseline prolactin variation, baseline corticosterone variation, hatching success or body condition of incubating female eiders in relation to individual and environmental explanatory variables after stepwise backward elimination.

Dependent variable	Explanatory variable	χ^2	P-value
Baseline prolactin concentration	Nest predation risk	4.570	0.033
Baseline corticosterone concentration	Breeding experience	14.359	< 0.001
	Clutch weight	7.094	0.008
	Nest predation risk	6.153	0.013
Hatching success	Baseline prolactin	5.333	0.021
	Radius-ulna length	3.101	0.078
	Female predation risk	4.278	0.039
	Nest predation risk	12.984	< 0.001
Female body condition at hatching	Breeding experience	8.738	0.003
	Female predation risk	4.506	0.034

Island identity was included as a random effect.

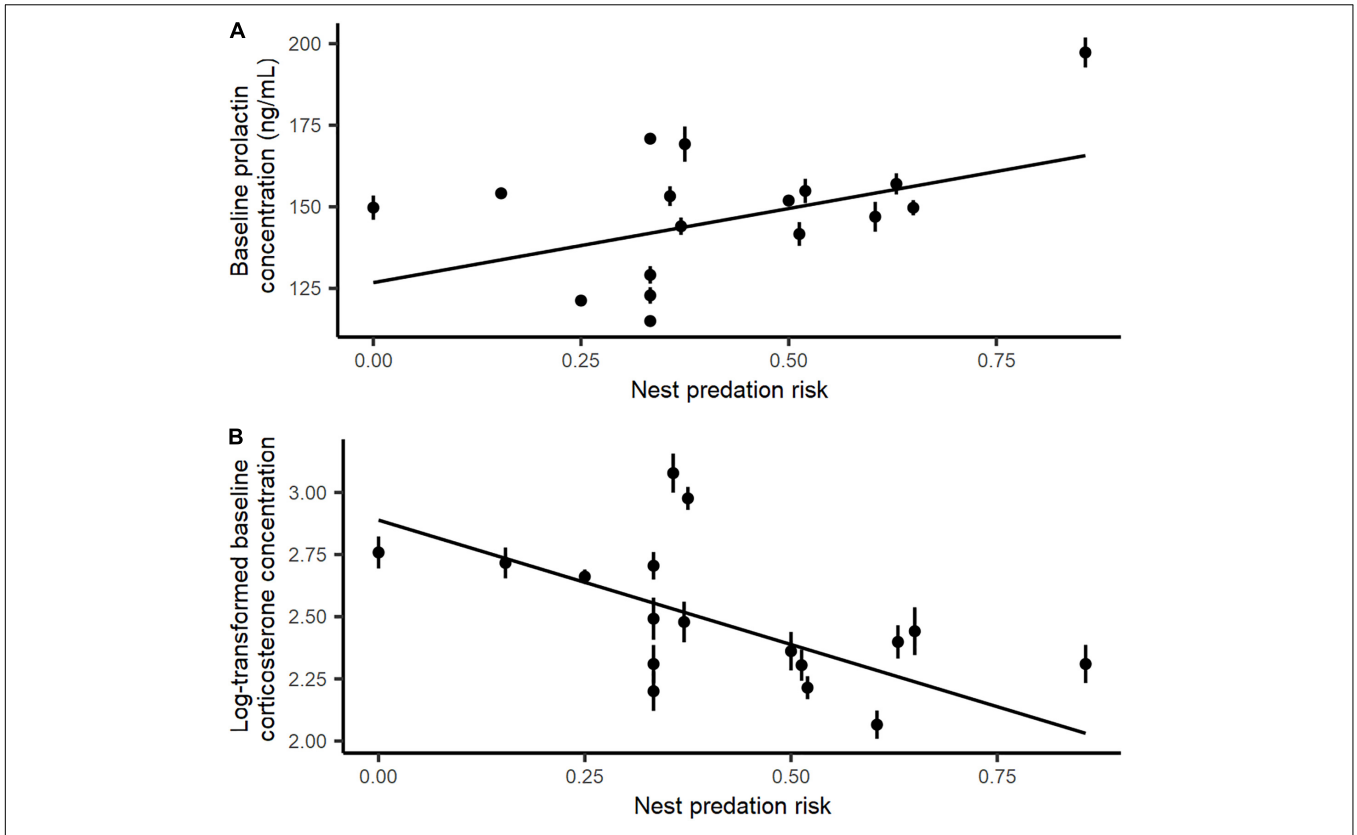


FIGURE 1 | Relationship between baseline (A) prolactin and (B) log-transformed corticosterone levels of incubating female eiders and island-specific nest predation risk. Black dots correspond to island-specific mean hormone levels and bars account for the standard error.

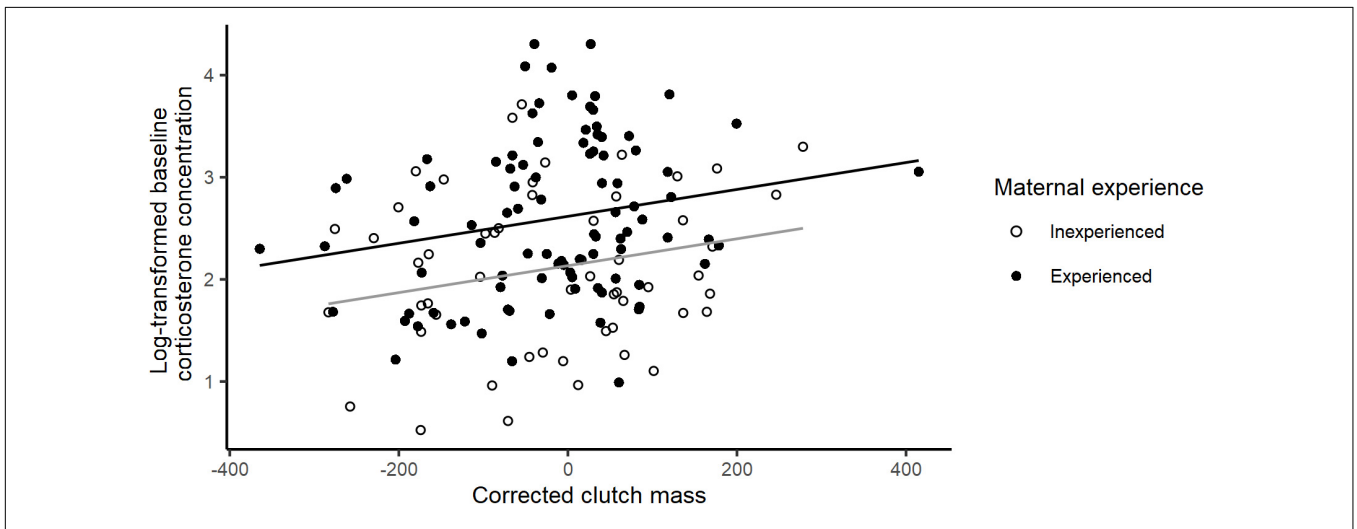
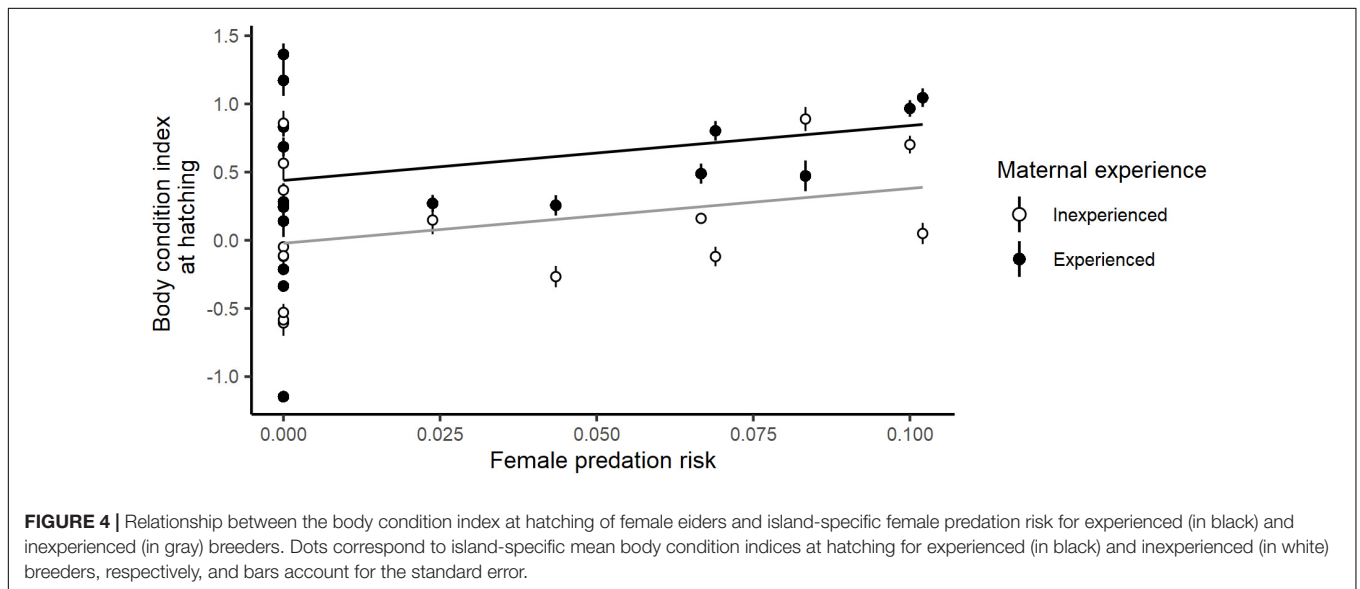
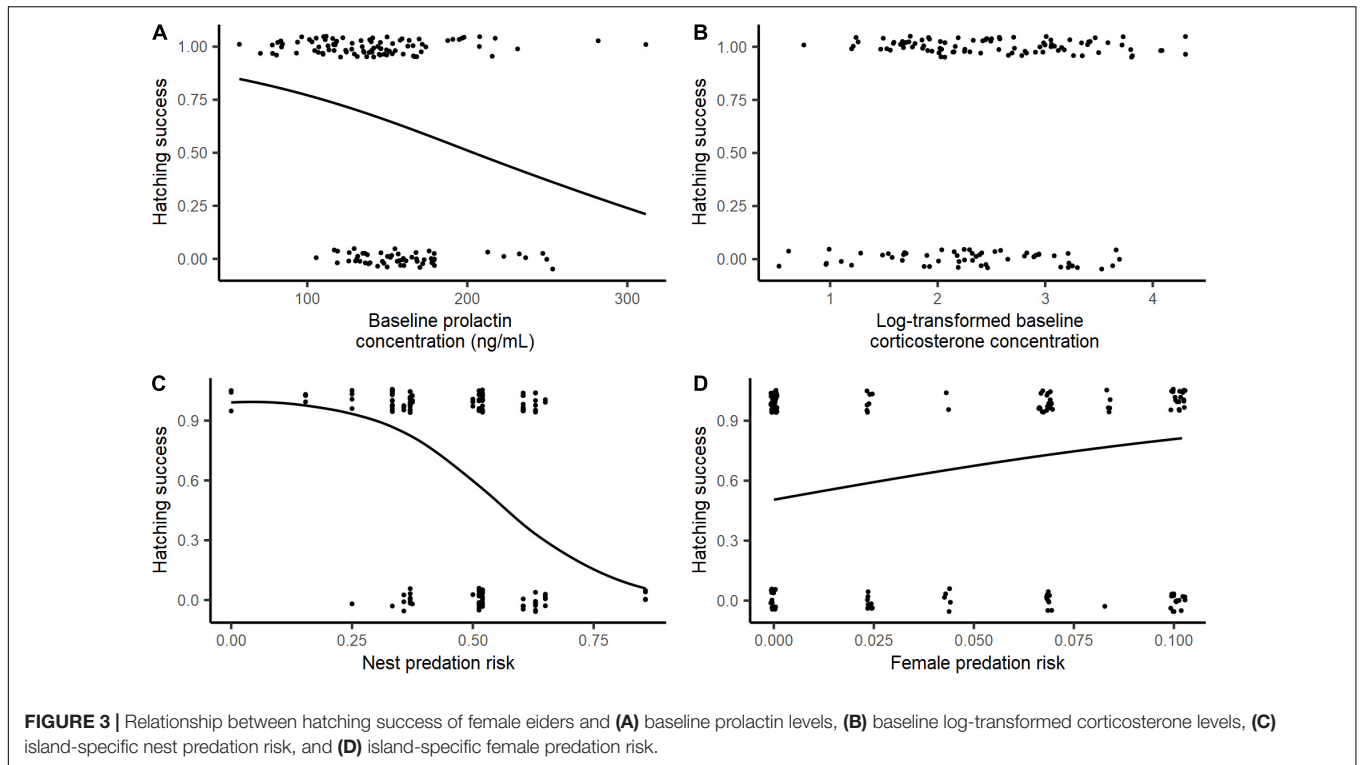


FIGURE 2 | Relationship between baseline log-transformed baseline corticosterone levels and incubation-stage corrected clutch weight of incubating female eiders for experienced (in black) and inexperienced (in gray) breeders.

DISCUSSION

In this study, we investigated the role of baseline prolactin and corticosterone levels, two hormonal correlates of parental investment (e.g., Criscuolo et al., 2002, 2005; Ouyang et al., 2013,

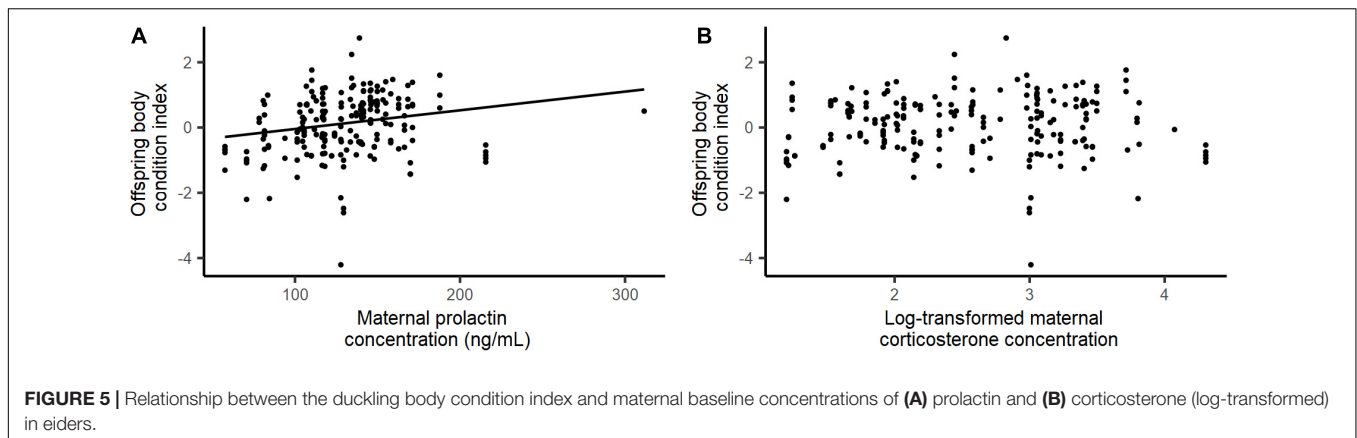
in modulating incubation commitment of female eiders in response to variable predation risk on themselves and their offspring. Baseline prolactin levels were unrelated to direct proxies of female quality (body condition and breeding experience) or reproductive investment (clutch weight).



However, elevated maternal prolactin levels were associated with better duckling body condition (Figure 5A), suggesting a positive association between female baseline prolactin levels and female parental commitment. Surprisingly, and contrary to our expectations, birds breeding on riskier islands (characterized by higher nest predation risk) displayed higher baseline prolactin levels. This unexpected finding may reflect an absence of low-quality individuals, characterized here by low prolactin levels, from risky nesting sites. In favor of this hypothesis, incubating females exposed to a higher threat of predation on themselves

were, on average, in better body condition (i.e., presumably of higher quality) than those nesting in less dangerous sites (Figure 4), even though we did not detect any direct association between female body condition and baseline prolactin levels.

In addition, we found that baseline corticosterone levels increased along with clutch weight, our proxy of energetic investment in reproduction, and was higher in experienced females than in inexperienced breeders. These two findings are in favor of the corticosterone-adaptation hypothesis and support the idea that elevated baseline corticosterone levels may



promote parental investment (Bonier et al., 2009). Accordingly, we found that birds breeding on islands with a high risk of nest predation displayed lower circulating corticosterone levels. Consequently, high nest predation risk and low prospects of successful hatching may lead females nesting in these risky areas to reduce their incubation commitment in the current clutch, through a lower allocation of resources to reproduction, mediated by lower baseline corticosterone levels.

Prolactin, Individual Quality, and Predation Risk

Contrary to our expectations, we found no influence of body condition at trapping, a proxy of individual quality, on baseline prolactin levels. This result suggests that, in incubating eiders, baseline prolactin levels are not directly affected by individual body condition. Although this result is not in line with the results from other studies (Crisuolo et al., 2002, 2003, 2006; Angelier and Chastel, 2009; Schmid et al., 2011), it could be explained by the non-linear link between prolactin and body condition in capital breeders (Drent and Daan, 1980). In such species, prolactin levels only decrease when individuals reach a very low threshold of body mass (Cherel et al., 1988). In our study, all individuals were above this threshold, which is around 1.10 kg for eiders (Korschgen, 1977). Accordingly, this lack of relationship between baseline prolactin levels and body condition has been highlighted in other capital-breeding birds with large amount of body reserves (Angelier et al., 2006; Verreault et al., 2008; Angelier and Chastel, 2009).

Likewise, and contrary to previous studies (Angelier et al., 2006, 2007b; Christensen and Vleck, 2008; Angelier and Chastel, 2009; Riechert et al., 2012; Smiley and Adkins-Regan, 2016), we did not find any significant increase in baseline prolactin levels with breeding experience, a proxy of individual quality in female eiders (Jaatinen and Öst, 2011). This discrepancy may result from the time of sampling: we caught all eiders toward the end of the incubation period, when a substantial fraction of the inexperienced breeders with low prolactin levels may already have failed. Overall, we did not find any direct evidence of a significant positive association between baseline prolactin levels and proxies of female quality (body condition and experience).

Higher prolactin levels were also not related to clutch weight (a proxy of energetic investment in reproduction), but they were positively associated with duckling body condition at hatching. This finding is noteworthy because the survival and recruitment of female eiders is related to their relative body condition as ducklings (Christensen, 1999), and thus the production of heavy offspring may have positive effects on maternal fitness. Altogether, these results suggest that maternal baseline prolactin levels may be positively associated with some but not all aspects of parental quality.

Baseline prolactin levels were positively associated with nest predation risk, but unrelated to adult predation risk and nest cover. This result is not in line with most studies evidencing lower prolactin levels in individuals subject to nest predation risk (Angelier et al., 2016). However, we showed that baseline prolactin levels were positively associated with duckling body condition, an indirect proxy of female quality, and this finding could indicate that only high-quality females were found on islands where nest predation risk was high. In line with this idea, we found that female body condition, a proxy of individual quality (Lehikoinen et al., 2010), increased along with adult predation risk. Two mutually non-exclusive explanations are possible. First, only high-quality females with high prolactin levels may opt to breed at risky sites in this species frequently exhibiting intermittent breeding (the reproductive suppression model; Wasser and Barash, 1983). Supporting this idea, a long-term analysis of female body condition at Tvärminne shows that body condition has been increasing over the past 15 years, concomitantly with a steeply increasing trend in white-tailed eagle numbers and in nest predation risk (Öst et al., 2018).

Second, higher baseline prolactin levels on risky islands could be explained by the early breeding failure of low-quality females on these sites. In our study, females were trapped toward the end of the incubation period and high prolactin levels and incubation commitment may be required to reach this stage of breeding on risky sites, whereas less committed females may reach this stage on safer islands. Indeed, prolactin is known to play a role in nest attendance and high prolactin levels are associated with lower tendency to abandon the nest (Spée et al., 2010; Angelier et al., 2016; Smiley and Adkins-Regan, 2018) and a shorter latency to

return to the nest after a disturbance (Angelier et al., 2009; Hope et al., 2020).

In addition, and contrary to both our *a priori* expectations and the previous literature (Angelier et al., 2007b, 2009, 2016; Ouyang et al., 2011; Riechert et al., 2014a), females displaying higher levels of baseline prolactin were less rather than more successful than those with lower levels. However, this result is consistent with the observed positive relationship between female prolactin levels and nest predation risk, likely arising from the selective disappearance of low-quality females with low baseline prolactin levels from the breeding pool on high-risk islands. Consequently, a putative link between high prolactin levels and high nest predation risk may lead to an indirect negative relationship between prolactin levels and reproductive success. In further support of this conclusion, there was a positive correlation between reproductive success and predation risk on adult females. This finding is consistent with the view that only high-quality females with high baseline prolactin levels opt to breed, or, alternatively, have nests that survive until the late incubation stage under high threat of predation. A positive correlation between female body condition at hatching and female predation risk (Figure 3D) is also consistent with this explanation. Summing up this evidence, we conclude that high-quality breeders characterized by high prolactin levels are likely to be overrepresented on risky sites at the end of the incubation period.

Corticosterone, Reproductive Investment, and Predation Risk

As for prolactin, we did not find any significant relationship between baseline corticosterone levels and female body condition. Such a lack of association between baseline corticosterone and body condition or body mass has also been shown in other eider populations (Bourgeon and Raclot, 2006; Criscuolo et al., 2006; D'Alba et al., 2011), and, more generally, in other capital breeders (Angelier et al., 2006; Groscolas et al., 2008). As for prolactin, this lack of a relationship could result from the fact that incubating female eiders have not reached a low threshold in body mass (Cherel et al., 1988) at the time of capture. However, we found that experienced breeders displayed higher baseline corticosterone levels than inexperienced breeders, a result in favor of the corticosterone-adaptation hypothesis (Bonier et al., 2009). Accordingly, some studies have found that circulating corticosterone levels increase with age and breeding experience in capital breeders with extended fasting periods (Angelier et al., 2006). In such species, elevated baseline corticosterone levels may be associated with an increased investment in reproduction, especially when individuals have not reached a lower threshold in body condition (Cherel et al., 1988), as is the case in our study.

In further support of the corticosterone-adaptation hypothesis, we found that baseline corticosterone levels were positively associated with clutch weight. Despite the possible occurrence of partial clutch predation (Erikstad et al., 1993; Öst et al., 2008) and conspecific nest parasitism, the

frequency of which is low in our population (ca 6% of eggs; Waldeck et al., 2004), clutch weight or size can be used as a reasonable proxy for female initial energetic investment in reproduction in eiders (Hanssen et al., 2003; Jaatinen et al., 2013). Overall, corticosterone may promote energy mobilization (Romero, 2002; Breuner, 2011) and incubation effort (Breuner, 2011; DuRant et al., 2013), and moderately elevated baseline corticosterone levels could be a proxy for increased incubation commitment in our study system. Accordingly, other studies have shown that increased baseline corticosterone levels do not trigger nest abandonment in eiders (Criscuolo et al., 2005), nor do they induce nest failure unless corticosterone levels reach very high values (D'Alba et al., 2011), a result consistent with the hormetic dose response framework (Costantini et al., 2010; Costantini, 2014). The positive association between baseline corticosterone levels and both clutch weight and maternal experience may thus indicate that incubating females increase their investment in a current reproductive event when its value is elevated (i.e., heavy clutch), and when the prospect of future reproduction diminish (the restraint hypothesis, Curio, 1983; Heidinger et al., 2006).

In addition, we showed that baseline corticosterone levels were negatively related to nest predation risk, but unrelated to adult predation risk and nest cover. These results are consistent with the corticosterone-adaptation hypothesis, and lower baseline corticosterone levels in risky nesting sites may therefore suggest that female eiders reduce their investment in incubation in the face of increased nest predation risk. This interpretation is supported not only by the fact that baseline corticosterone levels in this study were unrelated to hatching success and offspring quality, but also by the positive effect of breeding experience on both parental investment (Öst and Steele, 2010) and corticosterone levels in eiders (this study). Interestingly, similar effects of increasing nest predation risk on parental investment have been demonstrated in other species (Doligez and Clobert, 2003; Eggers et al., 2006; Zanette et al., 2011).

While baseline corticosterone levels can be seen as a proxy of parental investment, they can also mirror the response to prolonged exposure to chronic environmental perturbations, such as predation risk (Scheuerlein et al., 2001; Clinchy et al., 2004; Travers et al., 2010; Angelier and Wingfield, 2013). In that context, high baseline corticosterone levels could also be related to high stress sensitivity. Under that scenario, lower baseline corticosterone levels on risky sites could result not only from individuals reducing their parental investment under high predation threat, but also from the selective disappearance of highly sensitive individuals from these risky sites. Highly sensitive female eiders could either have already abandoned their breeding attempts prior to our trapping efforts on these sites, or they could have failed their breeding attempt at the time of trapping, toward the end of incubation. Females exhibiting higher baseline corticosterone levels would thus be expected to skip breeding more often and/or to be prone to abandon their nest when nesting on sites with a high risk of nest predation (Vitousek et al., 2014). Supporting this possibility, it has been found in other species that incubating individuals

displaying lower baseline corticosterone levels returned more quickly to the nest following a disturbance (Angelier et al., 2009; Edwards et al., 2013), or tended to abandon their nest less often than more sensitive individuals (Spée et al., 2010; Ouyang et al., 2012).

PERSPECTIVES

In this study, we investigated the role of baseline prolactin and corticosterone levels in modulating parental investment decisions under variable predation threat in incubating female eiders. We showed that birds breeding on islands subject to higher nest predation threat displayed higher baseline prolactin levels, and that this could reflect an absence of low-quality individuals with low prolactin levels at risky nesting sites. We also found that birds breeding on riskier islands displayed lower baseline corticosterone levels, and this may suggest that females reduce their incubation commitment on islands where predation risk on offspring is high (the corticosterone-adaptation hypothesis). Although our findings allow a better understanding of how predation risk may interact with hormonal regulation of parental investment, the correlative nature of the study does not allow us to draw causal relationships between hormone levels, parental investment and predation risk, highlighting the need for experimental studies to further clarify these relationships. In addition, our results do not allow us to distinguish effects of predation threat at the population level from effects of predation risk at the individual level. Longitudinal individual-based studies are now needed to disentangle within- and between-individual variation in hormonal levels in relation to individual quality and variable predation risk. This would allow us to distinguish natural selection processes from individual plasticity in responding to a changing environment. Such studies will eventually pave the way for a better understanding of the ability of prey to physiologically and behaviorally cope with environmental perturbations and how this impacts their reproductive life-history strategies.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the Handling of birds was approved by the National Animal Experiment Board (permit number ESAVI/1697/04.10.03/2012) and complied with the specific regulations of Tvärminne Zoological Station.

AUTHOR CONTRIBUTIONS

MÖ and KJ conceived the study and conducted fieldwork. CP and FA conducted laboratory analyses. BM analyzed the data. BM, MÖ, FA, and KJ interpreted the results. All authors contributed to writing the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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