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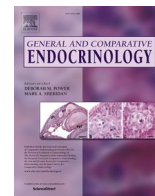
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Research paper

Parenting in a changing environment: A long-term study of prolactin, parental effort and reproductive success in common eiders

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ABSTRACT

Parental care is regulated by multiple endocrine mechanisms. Among these hormones, prolactin (PRL) is involved in the expression of parental behaviors. Despite the consensus that PRL mediates variation in parental effort with age and body condition, its role in the adjustment of parental effort to fluctuating environmental conditions, including changing predation pressure, still awaits further investigation. To shed light on this knowledge gap, we relied on a long-term monitoring of female common eiders *Somateria mollissima* ($n = 1277$ breeding attempts, 2012–2022) incubating under fluctuating predation risk to investigate the link between baseline PRL levels and female minimum age, body condition, clutch size, environmental parameters (predation pressure, climate, nest microhabitat) and hatching success. We predicted that PRL would be higher in older females, those in better condition or incubating larger clutches. We also predicted that females would reduce parental effort when nesting under challenging environmental conditions (high predation pressure or poor climatic conditions), translated into reduced baseline PRL levels. We also explored how variation in PRL levels, female characteristics and environmental parameters were related to hatching success. Following our predictions, PRL levels were positively associated with body condition and female age (before showing a senescent decline in the oldest breeders). However, we did not observe any population-level or individual-level reduction in PRL levels in response to increasing predation pressure. Population-level baseline PRL levels instead increased over the study period, coincident with rising predation threat, but also increasing female body condition and age. While we did not provide evidence for a direct association between baseline PRL levels and predation risk, our results support the idea that elevated baseline PRL levels promote hatching success under internal constraints (in young, inexperienced, breeders or those incubating a large clutch) or constraining environmental conditions (during years of high predation pressure or poor climatic and foraging conditions). Finally, the low repeatability of baseline PRL levels and high interannual variability highlight considerable within-individual flexibility in baseline PRL levels. Further research should explore flexibility in parental effort to changing environmental conditions, focusing on both baseline and stress-induced PRL levels.

1. Introduction

Parental care involves an array of parental behaviors that have evolved to increase offspring survival (Royle et al., 2012; Trivers, 1972), including nest building, production and incubation of eggs, and guarding and provisioning of offspring (Clutton-Brock, 1998). As investment

in current offspring results in a trade-off between current and future reproduction (i.e., a cost of reproduction) (Santos and Nakagawa, 2012; Stearns, 1992; Williams, 1966), parents are expected to be flexible in the amount and quality of parental care provided (Drent and Daan, 1980) – also referred to as parental effort. This can result in different parental strategies aiming to optimize fitness. Thus, breeding individuals are

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predicted to adjust parental effort to their state (e.g., age, experience or body condition; Erikstad et al., 1997; Testa and Adams, 1998; Pilakouta et al., 2015), the fitness value of the current reproductive event (e.g., clutch or brood value; Andersson et al., 1980; Dawson and Bortolotti, 2003; Sockman et al., 2007), as well as environmental conditions (e.g., nest concealment, climatic conditions, and predation pressure; Candolin, 1998; Conway and Martin, 2000; Malone et al., 2017; Weiser et al., 2018; Pelletier et al., 2023).

Parental care is regulated by multiple neural endocrine mechanisms (Buntin, 1996). Among these hormones, prolactin (PRL) plays a key role in the expression of parental and alloparental behavior (Angelier et al., 2016; Angelier and Chastel, 2009; Buntin, 1996; Smiley, 2019; Vleck and Vleck, 2011). Firstly, high PRL levels usually promote incubation behavior (e.g., Blévin et al., 2020; Hope et al., 2020; Thierry et al., 2013; Wang et al., 2020) as well as offspring provisioning (Duckworth et al., 2003; Schoech et al., 1996; Smiley and Adkins-Regan, 2016) and defense (Kindler et al., 1991; Pedersen, 1989; Wang and Buntin, 1999), potentially enhancing breeding success. Accordingly, successful breeders often display higher PRL levels than failed ones (Angelier et al., 2009a, 2013; Chastel et al., 2005; Crossin et al., 2012; Riou et al., 2010). In addition, low PRL levels are associated with nest desertion in several studies of wild birds (Groscolas et al., 2008; Angelier et al., 2015). Secondly, and importantly, PRL levels have been demonstrated to vary according to the parent's internal state. For example, PRL levels are usually higher in older or more experienced breeders (Angelier et al., 2006, 2007; Smiley and Adkins-Regan, 2016). PRL levels have also been shown to decrease in response to a depletion of body reserves (Angelier et al., 2013; Groscolas et al., 2008), especially when a minimum body condition threshold is reached (Cherel et al., 1994; Criscuolo et al., 2002). Finally, several studies have reported that PRL levels decrease in response to stress, that can be defined as when a biological control system detects a failure to control a fitness-critical variable, which may be either internal or external to the organism (Del Giudice et al., 2018) – although the definition of stress remains debated (Harris, 2020). Accordingly, PRL levels decrease under exposure to acute stressors (e.g., short-term stressors such as handling, restraints or injections; Angelier and Chastel, 2009) and circulating PRL levels are lower under chronic environmental stress (e.g., low food availability; Riechert et al., 2014a; drought; Delehanty et al., 1997), although data linking environmental conditions and PRL levels are lacking.

Despite the consensus that PRL can govern the parental behavioral response to acute stress and may mechanistically explain how parental care varies with age and body condition (Angelier et al., 2016; Angelier and Chastel, 2009; Smiley, 2019), its role in mediating parental adjustments to chronic environmental constraints – such as variation in predation pressure, availability of resources or climatic conditions – has been overlooked (reviewed in Angelier et al., 2016). Specifically, while parents are predicted to adjust reproductive effort to environmental conditions (Erikstad et al., 1998; Goodman, 1979), including to the risk of predation (Candolin, 1998; Malone et al., 2017), a limited number of studies have focused on PRL regulation in that environmental context. To shed light on this knowledge gap, we used an 11-year individual-based monitoring of female common eiders *Somateria mollissima* (hereafter, eiders) incubating under fluctuating predation pressure to investigate the link between baseline PRL levels, age, body condition, clutch size and environmental variables (predation pressure, climate, nest microhabitat). The study species exhibits exclusive female care, with females going through prolonged fasting during incubation, losing up to 46 % of their body mass (Parker, 1990). In this species and other fasting breeders, PRL levels remain elevated during the whole incubation period (e.g., Hector and Goldsmith, 1985; Vleck et al., 2000; Criscuolo et al., 2002) and PRL is thought to promote incubation commitment (Thierry et al., 2013; Hope et al., 2020; Wang et al., 2020). In addition, the study population in southwestern Finland, Baltic Sea, has been subject to a drastic change in predation regime, mainly due to the recovery of the white-tailed eagle *Haliaeetus albicilla* (hereafter, eagle),

which is the primary predator of incubating female eiders (Öst et al., 2022). Such a drastic increase in predation pressure has previously been linked to major changes in the eider population over the past decades, including variation in antipredator behavior (Mohring et al., 2022), physiology (Mohring et al., 2023), nesting habitat preferences (Ekroos et al., 2012; Mohring et al., 2022), as well as to an ageing of the population and an increase in intermittent breeding (Öst et al., 2018, 2022).

The combination of high energetic challenges associated with displaying exclusive female care and long-term fasting during incubation, coupled with a context of increasing but variable predation pressure, thus offers an ideal backdrop for further investigating the drivers of baseline PRL levels during incubation. Under the life-history assumption that long-lived animals should prioritize their own survivorship and opportunities for future reproduction over investment into the current reproduction (Roff, 1993; Stearns, 1992), we predicted that (1) the temporal increase in predation pressure on breeding individuals – linked to the recovery of eagle populations – would be associated with a decrease in female parental effort, and therefore, a reduction of baseline PRL levels. We further predicted that (2) PRL levels would vary according to female characteristics and reproductive effort (breeding experience, body condition and clutch size), being higher in experienced females, and in those in better condition or incubating larger clutches. Additionally, given our limited understanding of environmental influences on PRL secretion, we examined (3) whether and how environmental parameters (predation pressure, nest microhabitat and climate) shaped PRL levels, and also the relationships between PRL levels and female characteristics, and (4) the among-year intra-individual consistency of baseline PRL levels (i.e., repeatability). Last, we investigated (5) how variation in PRL levels, female characteristics and environmental conditions were related to hatching success.

2. Material and methods

2.1. Monitoring of breeding eiders

The study area comprised 22 islands in the vicinity of Tvärminne Zoological Station (59°50'N, 23°15'E, southwestern Finland, Baltic Sea). Between 2012 and 2022, three researchers equipped with a hand net thoroughly covered each island between mid-May and early June, detecting and attempting to catch all incubating female eiders. The monitoring period covered the mid- to late incubation period in this population, and was chosen in order to minimize the risk of nest abandonment following trapping (Bolduc and Guillemette, 2003).

Between 2012 and 2022, 1277 incubating females (corresponding to 681 unique individuals) were captured on their nests. Individuals were sampled on average (\pm SD) 1.9 (\pm 1.2) times (range 1–9 times) over the study period. Captured females were ringed with a unique metal ring and color-ring combination, sampled for blood from the ulnar vein (~1.5 mL), weighed (to the nearest 10 g using a Pesola spring balance) and their radius-ulna length was measured (to the nearest 1 mm using a wing ruler). During female handling, clutch size (mean \pm SD = 4.6 \pm 1.2 eggs, range 1–9) was recorded as a proxy of reproductive effort (Jetz et al., 2008; Stearns, 1992) and eggs were floated to estimate incubation stage (Kilpi and Lindström, 1997) (mean \pm SD number of days of incubation of captured females \pm SD = 17.4 \pm 4.9 days, range = 5.0–25.5 days). In the study area, females have been ringed when caught as first-time breeders since 1990, trapping effort has been constant and trapping success is high (since 1996, see Jaatinen and Öst, 2011; Öst et al., 2018). Thus, we used the number of years since the bird was ringed, to which we added three years – as female eiders on average start breeding when three years old (Baillie and Milne, 1982; Hario and Rintala, 2009; Nicol-Harper et al., 2021) – as a proxy of female minimum age (see further details of sample size and age over years in Supplementary material S1). In addition, we assessed female body reserves at the time of sampling by calculating an index of body condition, corresponding to the standardized residuals of a linear regression of log-transformed body weight on

log-transformed structural size (radius-ulna length) (linear model, LM, $t = 13.72$, $p < 0.001$).

Female eiders nest in a variety of microhabitats, ranging from fully open nests on rocky islets to nests concealed under dense vegetation cover (e.g., in juniper *Juniperus communis* bushes). To measure nest concealment, we took hemispherical photographs from the center of the nest cup using a 42-mm semi-fisheye lens mounted on an Olympus C-740 digital camera (Öst and Steele, 2010). Pictures covered lateral and vertical nest surroundings. They were converted to black (obstacle) and white (open sky) to allow the extraction of the proportion of nest cover (i.e., black pixels) as an index of nest concealment, with the software ImageJ (Abràmoff et al., 2004).

Eiders incubate for about 26 days (Korschgen, 1977). Based on egg floatation data, we predicted hatching date and revisited the nests at the estimated hatching date to monitor hatching success (0: failure, 1: success, $n = 1226$ nests with known fate). Duckling presence in the nest indicated hatching success. However, as eiders are precocial breeders and ducklings synchronously hatch and leave the nest within a day of hatching (Öst and Bäck, 2003), female and ducklings were not always present during nest revisits. In the absence of ducklings, eggshells and membranes were inspected to assess whether the breeding attempt was successful (intact leathery membranes) or failed (lack of eggshells or presence of eggshell pieces accompanied by bloody membranes, indicating nest depredation). A breeding attempt was considered successful if at least one duckling or one leathery membrane was found in the nest.

2.2. Baseline PRL assays

We sampled females for blood within 5 min and 30 s upon capture (mean \pm SD = 2 min 22 s \pm 0 min 25 s, range = 1 min 10 s – 5 min 14 s) to assess baseline PRL concentrations (Chastel et al., 2005). We centrifuged blood samples and stored blood serum at -20 °C until PRL radioimmunoassay was carried out at the Centre d'Etudes Biologiques de Chizé (CEBC) (10 assays, inter-assay CV: 12.05 %, intra-assay CV: 11.73 %). The radioimmunoassay method has previously been described (see Criscuolo et al., 2002) and validated for this eider population in a previous study analyzing one year of prolactin data from females sampled in 2013 (Mohring et al., 2021). All assays were run between November 2022 and January 2023 using the same reagents. In all assays, reference samples were run to control for inter-assay variation. It allowed us to check that all years of data were comparable and to calculate the inter-assay precision. In addition, samples from previous years were measured in the next runs to check that concentrations were consistent between assays and did not change through time. We verified that PRL levels did not significantly vary with sampling time (linear regression of PRL levels on sampling time, including year to control for interannual variation in PRL levels: $F = 0.04$, $p = 0.84$), to ensure that samples reflected baseline PRL concentrations.

2.3. Temporal variation in predation risk, climate and food availability

2.3.1. Predation risk

In the study area, the main predators of adult eiders are white-tailed eagles, American minks *Neogale vison* and raccoon dogs *Nyctereutes procyonoides* (Öst et al., 2018). However, depredation by American minks and raccoon dogs was low during the study period because of an intensive invasive alien predator removal scheme that has been carried out since 2011 (Jaatinen et al., 2022). In addition, eider eggs are depredated by hooded crows *Corvus cornix* and gulls *Larus* spp. – predominantly when the female is absent from the nest – or by predators of adult eiders following a predation attempt (Jaatinen et al., 2014; Hermansson et al., 2023).

Given that eagles are the main threat to incubating female eiders, we measured an index of eagle abundance – hereafter, eagle index – during the eider breeding season to quantify interannual variation in predation pressure and, more specifically, eagle activity at the study site. The eider

breeding season was considered to range from April 1 to June 15, i.e., the time from arrival on the breeding grounds to the end of incubation. The eagle index was calculated as the average daily number of resident eagles observed during this period. Resident eagles (including adults and immatures) were counted at Hanko Bird Observatory (HALIAS, 59°49'N, 22°54'E, ca 20 km from Tvärminne) by means of a standardized daily observation protocol (Lehikoinen et al., 2008; Öst et al., 2022). Given that white-tailed eagles – especially non-breeders – can travel long distances to forage (e.g., mean home range of non-territorial subadults: 180 km²; May et al., 2013), this index reflects the temporal variation in total white-tailed eagle abundance or activity in the study area, where none of the study islands is exempt from eagle predation.

2.3.2. Climate and food supply

Eiders are migratory birds. As a consequence, climatic conditions during winter are likely to have carry-over effects on reproductive performance (Descamps et al., 2010). Such effects are likely to be especially important given that eiders, as capital breeders, rely on endogenous reserves stored in the wintering grounds for egg production (Parker, 1990). However, recent evidence shows that eiders can also rely on local food supply to build energetic reserves before reproduction (Hobson et al., 2015; Jaatinen et al., 2016), and individuals differ regarding their use of stored (i.e., imported from the wintering areas) versus locally-ingested nutrients for reproduction (Jaatinen et al., 2016; Sénéchal et al., 2011). Therefore, this calls for the need to quantify interannual fluctuations in environmental conditions (food availability, harshness of climatic conditions) on both the wintering and breeding grounds. To this end, we combined meteorological data with a population-level index of female body condition at the start of incubation. In eiders, body condition of breeders at the start of incubation reflects the effect of variation in environmental conditions during the wintering and pre-breeding periods on food quality and quantity, which in turn affects the ability to store reserves for reproduction (Laursen et al., 2019; Rigou and Guillemette, 2010; Steenweg et al., 2022).

First, to characterize winter conditions, we relied on a global climatic index: the winter North Atlantic Oscillation (NAO). Winter NAO can be used as an indicator of meteorological conditions during winter. Positive values are associated with higher temperature and precipitation, as well as storminess in northern Europe (Hurrell, 1995; Matulla et al., 2008). Previous studies have indeed highlighted a link between winter NAO and eider body condition (Descamps et al., 2010; Lehikoinen et al., 2006). Second, as local breeding conditions may affect the contribution of local resources to reproduction (Hobson et al., 2015; Jaatinen et al., 2016; Sénéchal et al., 2011), we relied on meteorological data collected in the vicinity of Tvärminne to evaluate weather conditions during the eider breeding season. To this end, we used average daily temperature and total precipitation between April 1 and June 15. Climatic data were collected at Tvärminne Zoological Station and provided by the Finnish Meteorological Institute (FMI). Last, we calculated an annual index of population-level body condition at the start of incubation to characterize interannual variability in food supply. To allow comparison of body reserves of females at different stages of incubation (thus varying in fasting duration), we first estimated female body mass at the start of incubation by adding the mass lost during the days spent incubating to the mass of the female at trapping. Mass loss during incubation was obtained by multiplying the number of days spent incubating – estimated by egg floatation – by an estimation of daily mass loss (calculated as the slope of a linear regression of log-transformed body mass on incubation stage, LM, $t = -80.97$, $p < 0.001$). Then, we corrected female weight by female structural size by extracting the standardized residuals of a linear regression of log-transformed estimated weight at the start of incubation on log-transformed radius-ulna length (LM, $t = 32.81$, $p < 0.001$). Using these data, we calculated a population-level body condition index as the average yearly condition index of all monitored females.

We ran a principal component analysis (PCA, R function “PCA”,

FactoMineR package; Lê et al., 2008) to summarize annual fluctuations in climatic conditions and body condition. Variables included in the PCA were (1) winter NAO, (2) yearly mean temperature and (3) total precipitation during the eider breeding season, and (4) annual population-level body condition index at the start of incubation. All variables included in the PCA were centered and scaled. Following the brokenstick method (Frontier, 1976), only the first principal component was considered for further analysis. This principal component (PC₁) explained 62.2 % of interannual variation in environmental variables, and increasing PC₁ values were associated with low precipitation during the breeding season (correlation: $r = -0.93$, $p < 0.001$), lower winter NAO ($r = -0.88$, $p < 0.001$) and higher annual body condition at the start of incubation ($r = 0.79$, $p < 0.001$). Increasing PC₁ values indicate ‘good’ years, characterized by high population-level body condition at the start of incubation (i.e., good foraging conditions), low precipitation during the breeding season (i.e., clement weather) and a cold but dry winter preceding the breeding season.

2.4. Statistical analyses

Statistical analyses were conducted in R 4.3.1. (R Core Team, 2023). We implemented linear mixed models (LMMs, R function “lmer”, lme4 package; Bates et al., 2015) to investigate variation in baseline PRL levels and generalized linear mixed models with a binomial error distribution (GLMMs, R function “glmer”, lme4 package; Bates et al., 2015) to assess variation in hatching success. All quantitative independent variables were centered and scaled. We verified that the assumptions of normality and homoscedasticity of residuals were met by visually inspecting model residuals. We also verified the absence of multicollinearity among explanatory variables in the final models (all VIF < 2.0, i.e., below the conservative threshold of 2.5; Allison, 2012). Marginal R² (R_m², the variance explained by the fixed effects) and conditional R² (R_c², the variance explained by both the fixed and random effects) were calculated using R function “r.squaredGLMM” (MuMIn package; Barton, 2020).

2.4.1. Prolactin levels

We expected time trends in some of the variables tested as candidate predictors of PRL levels, such as female minimum age (Mohring et al., 2022; Öst et al., 2022), clutch size (Mohring et al., 2022), nest cover (Mohring et al., 2022), and eagle abundance (Öst et al., 2022). Therefore, we ran two separate analyses in order to (1) test for population-level temporal variation in baseline PRL levels and (2) investigate variation in PRL levels in relation to female characteristics and environmental variables.

First, we constructed LMMs with baseline PRL levels as the dependent variable and year either as a continuous or a categorical variable to test for a linear temporal trend or for non-linear, interannual variation in baseline PRL levels, respectively. Individual identity was included as a random effect to control for the non-independence of repeated observations of the same individual over the study period. We then compared the Akaike’s Information Criterion corrected for small sample size (AICc; Barton, 2020) of both models and of the null model to assess which model best fitted the data.

Second, we built LMMs with baseline PRL levels as the dependent variable and linear and quadratic female minimum age (to test for potential non-linear effects of age), body condition, clutch size, nest concealment, PC₁ and eagle index as independent variables. Incubation stage was added to the model to control for a potential increase in parental effort (and associated PRL levels) with increasing brood value (Santos and Nakagawa, 2012). In order to test for context-dependency in the relationships between PRL levels and age, body condition or clutch size, we included two-way interactions between each of the female characteristics (age, body condition and clutch size) and each of the environmental parameters (PC₁, eagle index and nest microhabitat). Individual identity and year were included as random effects to control

for the non-independence of samples collected on the same individual or during the same year. We ran all possible combinations of the candidate independent variables and interactions (R function “dredge”, MuMIn package; Barton, 2020) and performed model averaging (R function “model.avg”, MuMIn package; Barton, 2020) on the seven top-ranked models within $\Delta\text{AICc} < 2$ (see model details in Supplementary material S2). Last, we calculated within-individual adjusted repeatability of baseline PRL levels after controlling for potential effects of the aforementioned variables included in the full model (R function “rpt”, rptR package; Stoffel et al., 2017).

2.4.2. Hatching success

To assess the link between hatching success, baseline PRL levels, female characteristics and environmental fluctuations, we built GLMMs with a binomial error distribution, with hatching success as the dependent variable (0: failure, 1: success) and the interaction between female baseline PRL and environmental characteristics (PC₁, eagle index and nest cover) as well as the interaction between female baseline PRL and female characteristics (female minimum age and its quadratic term, body condition) or reproductive investment (clutch size) as independent variables. In addition, incubation stage – i.e., the number of days between the start of incubation and female trapping – was included as a covariate to control for variation in the total exposure time to predation risk, demonstrably affecting hatching success in the study system (Mohring et al., 2023). Female identity and year were included as random effects. We computed all possible combinations of the candidate independent variables and aforementioned interactions and performed model averaging on the four top-ranked models within $\Delta\text{AICc} < 2$ (see model details in Supplementary material S3).

3. Results

3.1. Population-level temporal trend in prolactin levels

The model testing for a linear trend in baseline PRL levels supported a linear increase of baseline PRL levels over the study period (LMM with year as a continuous variable: Estimate (E) ± standard error (SE) = 48.22 ± 3.62 , $t = 13.31$, $p < 0.001$; Fig. 1). Nevertheless, according to AICc values (Table 1), variation in PRL levels was best explained as non-linear, interannual variation (LMM with year as a categorical variable: $\chi^2 = 659.27$, $p < 0.001$), rather than by a linear temporal trend, as suggested by the model including year as a categorical variable outperforming both the null model ($\Delta\text{AICc}_{\text{M2-M0}} = 515.18$) and the model with year included as a numerical variable ($\Delta\text{AICc}_{\text{M2-M1}} = 352.84$). Based on R_m² values, the linear temporal trend accounted for 12 % of variation in baseline PRL levels, while non-linear year effects explained

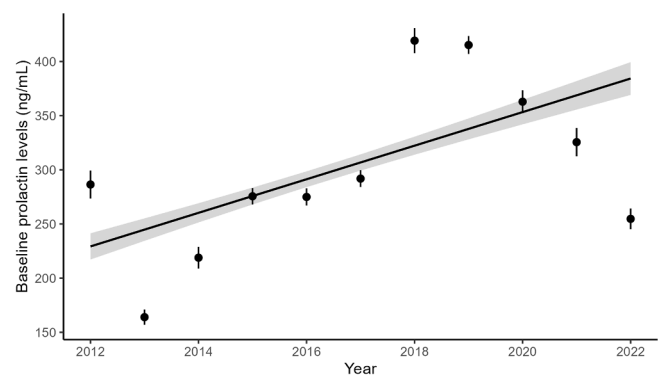


Fig. 1. Temporal variation in female common eider baseline prolactin levels during 2012–2022. Black dots correspond to yearly average population-level prolactin concentrations, and bars account for yearly standard errors. The regression line presents the significant linear temporal trend, and grey areas account for 95% confidence intervals.

Table 1

Model selection of linear mixed models testing for a null model (M_0), a linear temporal trend (year included as a continuous variable; M_1) or interannual variation (year included as a categorical variable; M_2) in female common eider baseline prolactin levels. Female identity was included as a random effect (1|ID) in all models. The model with the lowest AICc is presented in bold.

Model	df ¹	log-lik ²	AICc	ΔAICc	w _i ³	R ² _m ⁴	R ² _c ⁵
M₂	PRL ~ Year_{categorical} + (1 ID)	13	-7859.19	15744.67	0.00	1.00	0.34
M ₁	PRL ~ Year _{continuous} + (1 ID)	4	-8044.74	16097.51	352.84	0.00	0.12
M ₀	PRL ~ 1 + (1 ID)	3	-8126.919	16259.86	515.18	0.00	0.00

¹ df: degrees of freedom.

² log-lik: log-likelihood.

³ w_i: Akaike weight.

⁴ R²_m: marginal R², representing the variance explained by fixed effects.

⁵ R²_c: conditional R², representing the variance explained by both fixed and random effects.

34 % of variation in baseline PRL levels, indicating that baseline PRL levels vary between years in a non-linear way.

3.2. Intrinsic and extrinsic determinants of prolactin levels

After model averaging, the significant predictors of baseline PRL levels were quadratic female minimum age effects, female body condition at capture and the interaction between female body condition and PC₁ (Table 2). Baseline PRL levels peaked at an intermediate age, followed by a decrease in the oldest breeders (significant quadratic age effect, Table 2, Fig. 2). In addition, baseline PRL levels were positively correlated with female body condition at capture, and this relationship was more pronounced during ‘poor’ years, i.e., years characterized by low mean annual female body condition at the start of incubation, and a mild but stormy winter followed by a wet breeding season (female body condition × PC₁, Table 2, Fig. 3). We did not detect any significant relationship between baseline PRL levels and incubation stage, clutch size, nest concealment or the eagle index. In addition, within-individual adjusted repeatability of baseline PRL levels was significant but low (repeatability: R ± SE = 0.08 ± 0.03, 95 % confidence interval, CI = (0.04, 0.15), p < 0.001).

3.3. Hatching success, prolactin and predation

After model averaging, the significant and nearly significant predictors of hatching success were incubation stage and the two-way interactions between baseline PRL levels and female minimum age, clutch

Table 2

Model-averaged coefficient estimates and standard errors (E ± SE), z-values (z) and p-values (p) derived from the seven top-ranked LMMs (ΔAICc ≤ 2) explaining variation in female common eider baseline prolactin levels in relation to intrinsic attributes (incubation stage, female minimum age and its quadratic effect, body condition and clutch size), nest concealment (nest cover), annual environmental conditions (PC₁; positive values associated with high population-level body condition at the start of incubation and low winter NAO and precipitation during the breeding season), and annual predation risk (eagle index; average daily number of white-tailed eagles during the eiders’ breeding season) and the interactions between intrinsic attributes (female age and its quadratic effect, body condition and clutch size) and annual environmental conditions (nest cover, PC₁ and eagle index). Female identity and year were included as random effects. Significant effects (p-value ≤ 0.05) are presented in bold.

Fixed effect	E ± SE	z	p
Intercept	305.65 ± 22.60	13.53	< 0.001
Incubation stage	5.60 ± 4.84	1.16	0.248
Female minimum age	11.49 ± 4.66	2.47	0.014
Female minimum age²	-7.50 ± 2.58	2.91	0.004
Body condition	17.23 ± 4.31	3.99	< 0.001
Clutch size	-1.17 ± 3.13	0.37	0.710
Nest cover	-2.19 ± 3.28	0.67	0.504
PC ₁	6.45 ± 23.98	0.27	0.788
Eagle index	25.83 ± 19.57	1.32	0.187
Body condition × PC₁	-8.99 ± 3.07	2.93	0.003

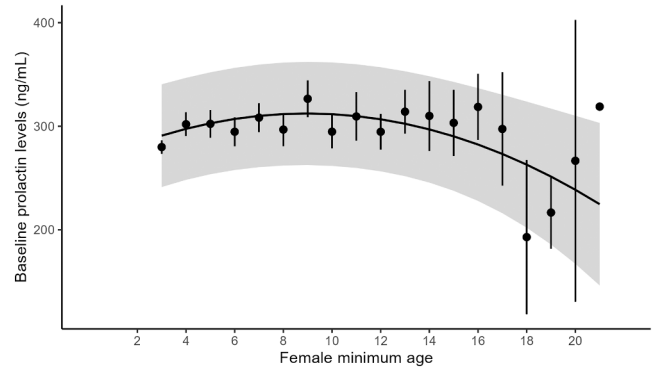


Fig. 2. Relationship between incubating female eider baseline prolactin levels and female minimum age (years of breeding experience). Black dots correspond to mean female baseline prolactin levels at each age, and bars account for standard errors. The regression line is presented in black, and grey areas account for 95% confidence intervals.

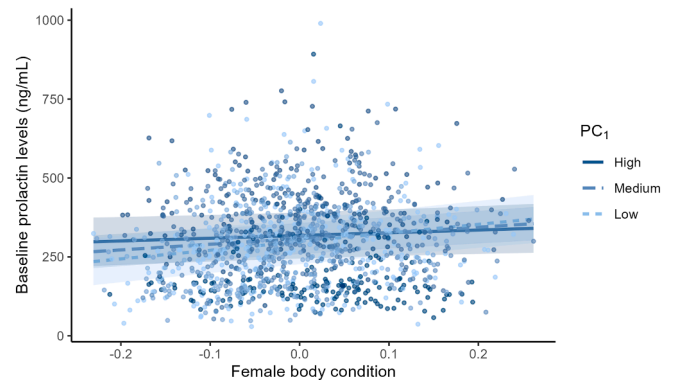


Fig. 3. Relationship between incubating female eider baseline prolactin levels and the interaction between female body condition at trapping and PC₁ (PC₁; positive values associated with high population-level body condition at the start of incubation and low winter NAO and precipitation during the eiders’ breeding season). The solid line denotes years with high PC₁ values (mean + 1 SD, corresponding to a year with ‘good’ environmental conditions), the dashed line years with intermediate PC₁ values (mean, corresponding to an ‘average’ year) and the dotted line years with low PC₁ values (mean - 1 SD, corresponding to a ‘poor’ environmental year).

size, eagle index and PC₁, respectively (Table 3). There was a trend towards higher baseline PRL levels in successful breeders at young age (baseline PRL × female minimum age, Table 3, Fig. 4A). Successful breeders also displayed higher baseline PRL levels than failed breeders when incubating a large clutch (baseline PRL × clutch size, Table 3, Fig. 4B). In addition, successful breeders were characterized by higher baseline PRL levels than failed breeders during ‘poorer’ years (baseline

Table 3

Model-averaged coefficient estimates and standard errors ($E \pm SE$), z-values (z) and p-values (p) derived from the four top-ranked GLMMs with a binomial distribution ($\Delta AICc \leq 2$) explaining variation in female common eider hatching success (0: failure, 1: success) in relation to female baseline prolactin levels, incubation stage, intrinsic attributes (female minimum years of maternal experience and its quadratic effect, body condition and clutch size), extrinsic attributes (nest cover, PC_1 ; positive values associated with high population-level body condition at the start of incubation and low winter NAO and precipitation during the eiders' breeding season and eagle index; average daily number of white-tailed eagles during the eiders' breeding season), the interaction between baseline prolactin levels and intrinsic attributes, as well as the interaction between baseline prolactin levels and extrinsic attributes. Female identity and year were included as random effects. Significant effects (p-value ≤ 0.05) are presented in bold and nearly significant effects (p-value ≤ 0.10) in bold and italic.

Fixed effect	$E \pm SE$	z	p
Intercept	0.48 \pm 0.09	5.37	< 0.001
Incubation stage	0.78 \pm 0.09	8.23	< 0.001
Baseline prolactin levels	0.10 \pm 0.08	1.24	0.215
Female minimum age	0.36 \pm 0.09	4.10	< 0.001
Clutch size	0.28 \pm 0.08	3.52	< 0.001
Body condition	0.06 \pm 0.12	0.49	0.624
Nest cover	-0.06 \pm 0.08	0.74	0.459
Eagle index	-0.11 \pm 0.09	1.24	0.215
PC_1	-0.14 \pm 0.08	1.84	0.066
Baseline prolactin levels \times Female minimum age	-0.16 \pm 0.09	1.83	0.068
Baseline prolactin levels \times Clutch size	0.23 \pm 0.08	2.79	0.005
Baseline prolactin levels \times Eagle index	0.30 \pm 0.09	3.21	0.001
Baseline prolactin levels \times PC_1	-0.23 \pm 0.07	3.09	0.002

PRL \times PC_1 , Table 3, Fig. 4C), as well as during years of high eagle abundance (baseline PRL \times eagle index, Table 3, Fig. 4D). Last, hatching success increased with advancing incubation stage at female capture (Table 3).

4. Discussion

Based on 11 years of monitoring of a long-lived seabird incubating under fluctuating predation pressure, we investigated – for the first time to our knowledge – the link between PRL levels, a hormonal proxy of parental effort, and predation risk. Intriguingly, and contrary to our prediction, we found that PRL levels fluctuated considerably over years at the population level, and tended to increase over the study period, despite increasing predation pressure and the concomitant expected reduction of parental effort. Baseline PRL levels were indeed found to be insensitive to variation in predation pressure, being primarily associated with female age and body condition (see 4.1). We also predicted that high PRL levels may be necessary to sustain hatching success, especially under increased predation risk or poor environmental conditions (see 4.2). Accordingly, we found that more successful breeders had higher PRL levels and that this relationship was more pronounced under internal constraints (i.e., in young and inexperienced breeders or when incubating a large clutch) and under constraining environmental conditions (i.e., during years of high predation pressure or years with poor foraging conditions; see 4.2). Finally, the low within-individual repeatability of baseline PRL levels of females sampled over multiple breeding attempts suggests that PRL levels are highly flexible and covary with several environmental and intrinsic variables.

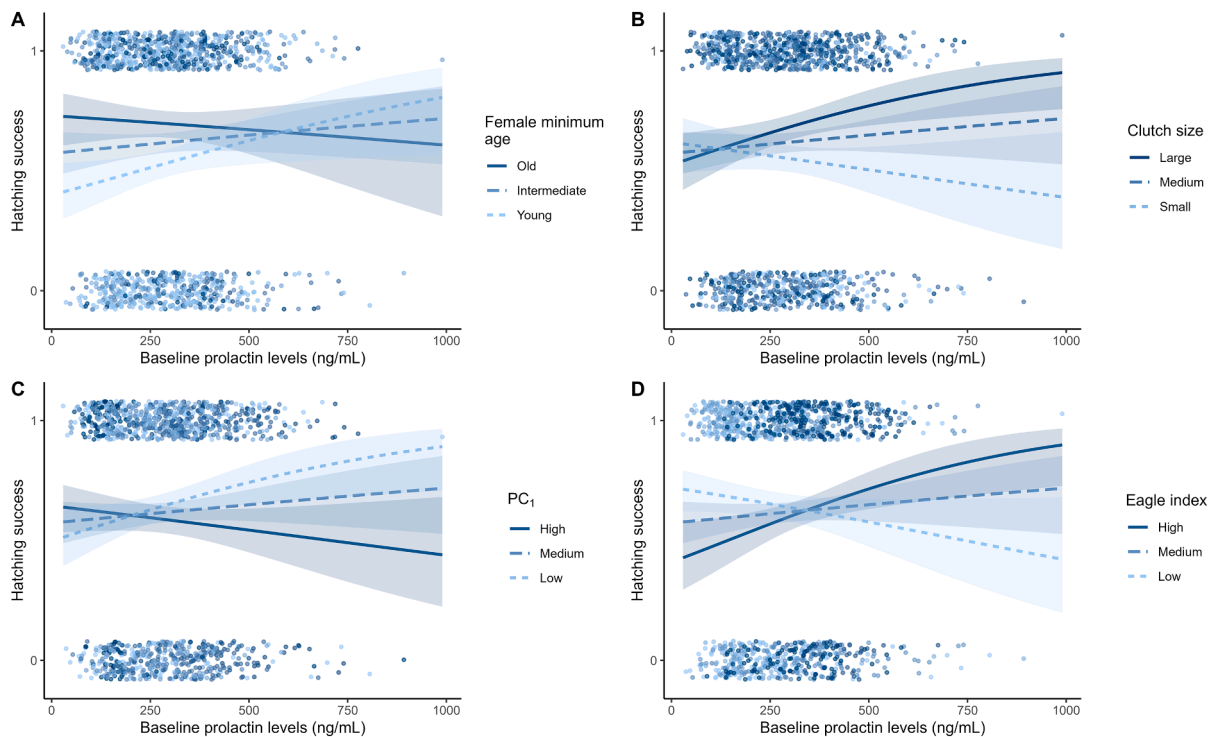


Fig. 4. Relationship between female common eider hatching success (0: failure, 1: success) and the interaction between female baseline prolactin levels and (A) female minimum age, (B) clutch size, (C) PC_1 (positive values associated with high population-level body condition at the start of incubation and low winter NAO and precipitation during the eiders' breeding season) and (D) annual predation risk (eagle index; average daily number of white-tailed eagles during the eiders' breeding season). The solid line denotes (A) old females, (B) large clutches, (C) years of high PC_1 values or (D) eagle abundance (mean + 1 SD), the dashed line denotes intermediate (A) age, (B) clutch size, (C) PC_1 values or (D) eagle abundance (mean) and the dotted line (A) young females, (B) small clutches, years with (C) low PC_1 values or (D) low eagle abundance (mean - 1 SD).

4.1. State- and context-dependency of baseline prolactin levels

First, intermediate-aged individuals displayed higher baseline PRL levels. This finding is in agreement with the expected increase in reproductive investment with age, as residual reproductive value decreases (Clutton-Brock, 1984; Williams, 1966), supported by ample empirical evidence (Angelier et al., 2006, 2007a, 2007b; Riechert et al., 2012; Schradin and Pillay, 2004; Smiley and Adkins-Regan, 2016; Ziegler et al., 1996). Importantly, this increase was followed by a decrease in PRL levels in the oldest females that possibly indicates physiological senescence. While the relationship between age and PRL has been extensively studied, this is, to our knowledge, among the first, albeit cross-sectional, evidence of senescence in baseline PRL levels in the wild (but see Angelier et al., 2007b). Accordingly, Angelier et al., (2007b) reported a decrease in both baseline PRL levels and breeding success in the oldest and most experienced breeding black-browed albatrosses, *Thalassarche melanophris*. Interestingly, we here highlighted an age-specific pattern of PRL variation despite the use of an estimate of apparent age (based on the year of ringing), rather than real female age. This suggests that age effects could be even stronger. Noteworthy, the observed age effect could be driven by both within-individual change and selective disappearance. However, empirical evidence suggests that selective disappearance of poorly performing individuals may mask rather than induce aging-related declines in physiological function or reproductive performance, and actual senescence is therefore thought to begin earlier when selective disappearance effects are accounted for (Bouwhuis et al., 2009). In further support of the senescence hypothesis, baseline PRL levels were found to exhibit low repeatability within individuals, suggesting that selective disappearance could not fully account for the reported decrease in PRL levels in very old eiders.

Second, we found that females in poor condition displayed lower baseline PRL levels. This result aligns with the idea that parents in poor body condition should reduce or terminate parental investment to promote their own survivorship (Groscolas et al., 2008; Ledwoń et al., 2023; Wiggins et al., 1994). Such redirection of body reserves from reproduction towards survival is likely to be facilitated by a downregulation of PRL levels (O'Dwyer et al., 2006). Although poor body condition does not always correlate with reduced baseline PRL levels (Angelier et al., 2009b, 2013), the observed negative association between parent nutritional status and baseline PRL levels is supported by previous findings (Riechert et al., 2012; Schmid et al., 2011), notably in seabirds relying on prolonged fasting periods (Angelier and Chastel, 2009; Criscuolo et al., 2002, 2006; Groscolas et al., 2008; O'Dwyer et al., 2006; Riechert et al., 2012). In addition, Riechert et al., (2014b) showed that common terns *Sterna hirundo* had lower PRL levels after fasting during an incubation bout than when returning satiated from a foraging trip, a result in agreement with the idea of a functional link between parent nutritional status and baseline PRL levels (Angelier et al., 2016).

Interestingly, we found that the association between poor female body condition and low baseline PRL levels was accentuated during 'poor' years (i.e., negative PC₁ scores), characterized by low population-level body condition at incubation onset, a positive winter NAO index (i.e., mild but stormy winters) and high rainfall during the breeding season (female body condition at trapping \times PC₁; Fig. 3). Because higher sea water temperature during mild winters negatively affects blue mussel condition at winter and early spring foraging sites (Waldeck and Larsen, 2013), and since mussel beds can be destroyed by winter storms (Commito and Dankers, 2001; Reusch and Chapman, 1995), positive winter NAO years are likely to reflect poor foraging conditions for sea ducks. This is further reflected in the negative correlation between winter NAO values and population-level body condition at the start of incubation. In addition, high rainfall during the breeding season could induce a greater energetic need for thermoregulation during incubation (Clutton-Brock, 1991; Skagen and Adams, 2012). While the impact of fluctuating environmental conditions on baseline PRL levels has been overlooked (but see Delehanty et al., 1997; Rubenstein et al., 2008;

Riechert et al., 2014a; Smith et al., 2023), our findings corroborate the few studies suggesting an influence of food supply (herring and sprat abundance; Riechert et al., 2014a; trophic level; Smith et al., 2023) or climatic conditions (rainfall; Rubenstein et al., 2008; severe drought; Delehanty et al., 1997) on PRL levels.

Contrary to our predictions, we found no significant relationship between baseline PRL levels and clutch size or incubation stage – proxies of the reproductive value of the current breeding event (Albrecht and Klvaňa, 2004). This result suggests that despite increased egg stimuli from incubating a larger clutch, baseline PRL levels may not be driven by clutch size *per se*. A similar lack of association between clutch size and PRL levels during incubation has been reported in other studies (Hope et al., 2020; Ruiz-Raya et al., 2018; Silverin and Goldsmith, 1983; Smiley and Adkins-Regan, 2016), including an experimental one manipulating clutch size during incubation in eiders (Criscuolo et al., 2006). The elevation of circulating PRL levels at the end of egg laying may instead reflect a transition from egg-laying to incubation behavior (Angelier et al., 2016; Sockman et al., 2007), and PRL levels may then remain elevated during incubation independently of clutch size. Indeed, in precocial species, PRL levels have been shown to rapidly increase following egg laying, remain high during incubation and decline after chick hatching (Buntin, 1996; Smiley, 2019). This pattern has previously been described in eiders (Criscuolo et al., 2002) and would explain the observed lack of association between female baseline PRL levels and incubation stage. Alternatively, but non-exclusively, we may have lacked individual variation in incubation stage to detect any effect of incubation stage on PRL levels. Indeed, all female eiders were sampled during the latter half of incubation (mean \pm SD = 17.4 \pm 4.9 days of incubation).

4.2. State- and context-dependent link between prolactin and hatching success

Despite the predicted reduction in parental effort in response to increased predation risk (Candolin, 1998; Malone et al., 2017) – presumably orchestrated by reduced baseline PRL levels – baseline PRL levels did not decrease over the study period. Instead, baseline PRL levels showed high interannual variability and even a temporal increase. This result is consistent with our previous short-term study, in which we investigated the association between female eider baseline prolactin levels, predation risk and direct and indirect proxies of female quality and investment in reproduction, using one year of prolactin data from females sampled in 2013 (Mohring et al., 2021). In this study, we found a positive correlation between baseline PRL and predation risk (Mohring et al., 2021). In that study, we argued that elevated PRL levels under increasing threat of predation may reflect the selective disappearance of low-quality breeders with low PRL levels. Nevertheless, predator-induced selective disappearance is unlikely to be the main driver of the positive time trend in population-level baseline PRL levels. Indeed, we found in this study that baseline PRL levels were insensitive to variation in annual predation risk, as quantified by the eagle index, as well as to variation in nest concealment, providing shelter from visual predators. In addition, the low within-individual repeatability of baseline PRL levels suggests that PRL levels are highly flexible. At the population scale, the temporal increase in baseline PRL levels may thus be primarily driven by other concomitant changes in the population, such as an increase in the body condition (Mohring et al., 2022; Öst et al., 2018) and age (Mohring et al., 2022; Öst et al., 2022) of breeding females. Additionally, unknown environmental changes may play a role, as baseline PRL levels appear to fluctuate widely between years (this study; Delehanty et al., 1997; Rubenstein et al., 2008; Riechert et al., 2014a, 2014b).

Our findings consistently showed that displaying elevated baseline PRL levels seemed particularly beneficial for reproductive success under challenging intrinsic or extrinsic conditions – whether these challenges were related to limited breeding experience (measured by female age;

Fig. 4A), the cost of incubating a large clutch (indexed by clutch size; Fig. 4B), climatic and resource constraints (assessed through PC₁; Fig. 4C) or to predation risk (measured by the eagle index; Fig. 4D). Elevated baseline PRL levels may thus promote more attentive incubation behavior in young birds with little previous breeding experience, increasing the chances of reproductive success. In addition, maintaining high baseline PRL levels may be beneficial under energetically-challenging conditions associated with fasting during incubation or incubating a large clutch, by promoting incubation constancy and inhibiting nest desertion. High baseline PRL levels may buffer the detrimental effects of poor environmental conditions or high predation pressure on hatching success. Given that low PRL levels have previously been associated with nest or chick abandonment (Chastel and Lormée, 2002; Groscolas et al., 2008; Spée et al., 2011, 2010), as well as egg neglect (Angelier et al., 2015), we hypothesize that high PRL levels may also be beneficial under high predation risk by helping breeders to resume incubation behavior following failed predation attempts or false alarms. In accordance with this idea, previous studies have demonstrated or suggested a shorter latency to return to the nest after a disturbance or higher nest attendance in parents displaying higher baseline PRL levels (Angelier et al., 2009a, 2015; Criscuolo et al., 2005). Overall, these results show the importance of considering individual characteristics and extrinsic environmental conditions when investigating the relationship between PRL levels and reproductive success.

In addition to baseline PRL levels themselves, it is important to note that the effects of PRL on physiology, behavior or life-history are mediated by prolactin receptors (Farrar et al., 2022; Smiley et al., 2021, 2020). These receptors are still poorly known, and recent findings suggest that they can vary in density, both among individuals and during an individual's lifetime (Farrar et al., 2022; Smiley et al., 2021, 2020). Therefore, the association between baseline PRL levels and hatching success may further depend on the activation of prolactin receptors, explaining the variance remaining unexplained after accounting for intrinsic and extrinsic covariates in our final models (Supplementary material S2 and S3).

5. Conclusions

The low individual repeatability of baseline PRL levels ($R \pm SE = 0.08 \pm 0.03$) reflects either a lack of among-individual differences or high within-individual variation in PRL. Our study argues in favor of the latter explanation, as we found that strong interannual variability was a key feature affecting baseline PRL levels, in agreement with previous studies (Delehanty et al., 1997; Riechert et al., 2014a, 2014b; Rubenstein et al., 2008). Individual flexibility in baseline PRL levels may enable individuals to cope with constraining extrinsic or intrinsic conditions during incubation. This idea was notably supported by the finding that females displaying elevated baseline PRL levels had a higher probability of hatching success than females displaying lower PRL levels when breeding during years characterized by poor climatic conditions and food resources or high predation pressure. However, due to the cross-sectional nature of the study, within-individual flexibility in baseline PRL levels in response to gradients of environmental conditions still awaits further investigations. As exposure to acute stressors is known to trigger a decrease in circulating PRL levels (Chastel et al., 2005; Gratto-Trevor et al., 1991; Ruiz-Raya et al., 2018), the magnitude of the reduction of PRL levels in response to a standardized stress protocol may provide additional information on the role that PRL plays in the adjustment of parental effort to rapidly changing environmental conditions (Angelier and Chastel, 2009). We thus encourage further studies exploring stress-induced variation in PRL levels under changing predation risk to assess the resilience of prey individuals to fluctuating environmental conditions.

CRedit authorship contribution statement

Bertille Mohring: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. **Markus Öst:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Kim Jaatinen:** Conceptualization, Funding acquisition, Investigation, Project administration, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing. **Charline Parenteau:** Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Marie Pallud:** Formal analysis, Writing – original draft, Writing – review & editing. **Frédéric Angelier:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ygcen.2024.114574>.

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* studies carried out on the same population

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