Environmental Research 303 (2026) 124643

Contents lists available at ScienceDirect

Environmental Research

journal homepage: www.elsevier.com/locate/envres

Nest attendance in two Finnish waterfowl species in relation to per- and polyfluoroalkyl substances and thyroid hormones

Farshad S. Vakili [a,*], Scott A. Shaffer [b], Veerle L.B. Jaspers [c], Silje Peterson [a], Elise Lunde Steensland [c], Pentti Runko [d], Bertille Mohring [e,f,g], Markus Öst [e,h], Kim Jaatinen [i], Bin-Yan Hsu [j], Titiksha Peetumber [a], Nora M. Wilson [k,l], Christian Sonne [m], Stefan Björkman [n], Suvi Ruuskanen [o], Céline Arzel [a,p]

[a] Department of Biology, University of Turku, Vesilinnantie 5, 20014, Turku, Finland
[b] San José State University, Department of Biological Sciences, San Jose, CA, USA
[c] Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, NO-7491, Trondheim, Norway
[d] Hirvipurontie 44, Maaninka, Finland
[e] Environmental and Marine Biology, Åbo Akademi University, Turku, Finland
[f] Centre d'Etudes Biologiques de Chizé (CEBC), UMR, 7372, CNRS – Université de La Rochelle, Villiers-en-Bois, France
[g] School of Environmental Sciences, University of Liverpool, Liverpool, UK
[h] Novia University of Applied Sciences, Ekenäs, Finland
[i] Finnish Environment Institute (SYKE), Latokartanonkaari 11, 00790, Helsinki, Finland
[j] Department of Life Science, Tunghai University, Taichung, Taiwan
[k] Ab Bengtskär Oy, FI-25950, Rosala, Finland
[l] Physics, Faculty of Science and Engineering, Åbo Akademi University, Turku, Finland
[m] Department of Ecoscience, Aarhus University, DK-4000, Roskilde, Denmark
[n] Department of Production Animal Medicine, Faculty of Veterinary Medicine, University of Helsinki, Helsinki, Finland
[o] Department of Biological and Environmental Sciences, University of Jyväskylä, Finland
[p] OMPO, 59 rue Ampère, Paris, France

ARTICLE INFO

Keywords:
Endocrine disruption
Incubation behaviour
Forever chemicals
Reproduction
Thyroid hormones
Waterfowl

ABSTRACT

Contamination of aquatic environments with per- and polyfluoroalkyl substances (PFAS) may disrupt wildlife reproduction by altering hormonal-behavioural pathways. In birds, nest attendance is a key incubation behaviour, mediating embryonic development and hatchability. Yet, the potential associations between PFAS and nest attendance remains underinvestigated. In 2022 and 2023, we quantified plasma PFAS concentrations in breeding females from two Finnish waterfowl species: common goldeneyes (*Bucephala clangula*), an income breeding cavity nester, and common eiders (*Somateria mollissima*), a predominantly capital breeding ground nester. Egg-turning and egg temperature were recorded using data loggers inside artificial eggs. We related these nest attendance variables to PFAS and circulating thyroid hormones (THs: triiodothyronine (T3), thyroxine (T4)), as previous studies showed that PFAS exposure is associated with altered levels of THs—key regulators of metabolism and thermoregulation. Mean PFAS concentrations were 17.4 ng/g in goldeneyes (n = 18) and 16.2 ng/g in eiders (n = 37). In eiders, higher perfluorooctanesulfonic acid (PFOS) concentrations were significantly associated with lower average egg temperature. Exploratory post hoc analyses (following marginal PFAS × species interaction trends) suggested positive associations between total PFAS (∑PFAS) and PFOS with egg-turning frequency in goldeneyes. No significant associations were found between PFAS and THs, and THs were not significantly associated with nest attendance. PFAS were not significantly related to hatching success. Further research is needed to determine if species-specific PFAS-nest attendance associations reflect trade-offs with other PFAS-related behavioural or physiological costs. Experimental studies may be necessary to clarify PFAS-thyroid and physiological stress pathways and their consequences for nest attendance and reproduction.

* Corresponding author. Department of Biology, University of Turku, Finland.
E-mail addresses: Sajjad.s.vakili@utu.fi, Farshad.s.vakili@gmail.com (F.S. Vakili).

https://doi.org/10.1016/j.envres.2026.124643
Received 9 February 2026; Received in revised form 14 April 2026; Accepted 30 April 2026
Available online 5 May 2026

1. Introduction

Increasing contamination of aquatic environments with per- and polyfluoroalkyl substances (PFAS) is a major concern for human and wildlife reproduction (Lohmann et al., 2024). PFAS are a large group of anthropogenic amphiphilic compounds that are highly persistent in the environment owing to strong carbon-fluorine (C-F) bonds (Byns et al., 2022). Some PFAS are capable of long-range transport via water currents and atmospheric deposition (Buck et al., 2011). Consequently, aquatic ecosystems worldwide are exposed to varying levels of PFAS (Xiao, 2017; Banyoi et al., 2022), where biomagnification may occur across trophic levels (Banyoi et al., 2022; Ricolfi et al., 2024) through accumulation in invertebrates, fish and higher trophic-level avian species (Byns et al., 2022).

A growing number of recent wildlife studies have reported measurable concentrations of several PFAS compounds in waterfowl (for review; Sun et al., 2023). This is expected, as waterfowl occupy relatively high trophic positions and can therefore serve as bioindicators for anthropogenic PFAS, which bioaccumulate through dietary uptake (Robuck et al., 2020; Vainio, 2022). The Baltic Sea, our study area, is among the most contaminated marine systems globally due to human activities (Sonne et al., 2020). Complex PFAS mixtures have been detected in Baltic waterfowl, including Finnish populations of common goldeneye (*Bucephala clangula*) and common eider (*Somateria mollissima*) (Frøyland, 2022; Lunde, 2023).

Empirical and experimental animal studies have documented PFAS effects on survival, endocrine disruption and physiological toxicity, with potential consequences for reproductive performance. For instance, direct mortality caused by dietary exposure to perfluorooctanesulfonic acid (PFOS) has been reported in mallard (*Anas platyrhynchos*) ducklings (Newsted et al., 2007), and in avian embryos exposed to PFOS and perfluorooctanoic acid (PFOA) (Nordén et al., 2016; Bursian et al., 2021). Several PFAS compounds have been linked with altered thyroid hormone levels (THs). For example, exposure to PFAS mixtures reduced embryonic THs in chicken (Mattsson et al., 2019), whereas multiple PFAS—including perfluorohexanesulfonic acid (PFHxS), perfluorodecanesulfonic acid (PFDS), PFOA, perfluorotetradecanoic acid (PFTeDA), and perfluorohexadecanoic acid (PFHxDA)—were positively associated with THs in peregrine falcon (*Falco peregrinus)* nestlings (Sun et al., 2021). In addition to endocrine disruption, several long-chain PFAS, such as perfluorododecanoic acid (PFDoDA), perfluorotridecanoic acid (PFTriA), PFTeDA, and perfluoroundecanoic acid (PFUnA), have been associated with oxidative stress, in male black-legged kittiwakes (*Rissa tridactyla*; Costantini et al., 2019). Despite this physiological evidence, research incorporating behavioural endpoints remains limited.

PFAS exposure has been associated with changes in reproductive behaviour, potentially involving multiple physiological pathways. For instance, physiological stress caused by PFOS and PFOA has been shown to alter motor function in laboratory rodents (as reviewed by Brown--Leung and Cannon, 2022). Similarly, PFOS exposure has been linked to spontaneous hyperactivity in zebrafish (Spulber et al., 2014). Another proposed pathway for PFAS influence on behaviour involves endocrine disruption, whereby PFAS interfere with hormonal regulation and may consequently affect behaviour (McNabb, 2007; Sebastiano et al., 2021). To our knowledge, only one study in wildlife has examined the relationship between PFAS burden and reproductive behaviours in a free-living bird, showing that PFOS and several perfluoroalkyl carboxylic acids (PFCAs) were associated with incubation behaviour in black-legged kittiwakes (Blevin et al., 2020).

Incubation is a critical period in avian reproduction, during which parental behaviour and physiological state jointly influence egg-turning and temperature maintenance, both of which are linked to embryonic development. These processes may vary with environmental conditions, including PFAS contamination. Egg-turning is essential for heat distribution and for preventing albumin stratification and adhesion of the yolk and embryo to the inner egg-shell (Deeming, 2009). The study by Blevin et al. (2020) remains the single field study directly linking PFAS contamination to egg-turning behaviour. They reported a positive correlation between PFOS and perfluorononanoic acid (PFNA), with egg-turning frequency; and PFOS, PFNA, PFUnA, and PFTriA positively correlated with angular changes of the eggs Because incubation is under endocrine regulation, a key unresolved question is whether PFAS-associated changes in nest attendance could reflect endocrine alteration. In the same study on black-legged kittiwakes (Blevin et al., 2020), circulating prolactin—a peptide hormone involved in stimulation and maintenance of parental care in birds—was positively associated with egg-turning behaviour. Conversely, experimental suppression of prolactin using the dopamine D_2 agonist bromocriptine increased egg-turning rates in Adélie penguins (*Psygoscelis adeliae*) (Thierry et al., 2013a). In wood ducks (*Aix sponsa*) higher prolactin was associated with higher incubation constancy and egg temperature (Hope et al., 2020). Additionally, corticosterone manipulation negatively affected egg temperature in Adélie penguins (Thierry et al., 2013a, 2013b). These studies highlight that multiple endocrine axes can influence nest attendance in birds.

Notably, potential associations between parental thyroid hormones and nest attendance behaviour have not yet been examined. Existing studies have mainly manipulated incubation temperature and investigated effects on offspring THs (DuRant et al., 2014; Hope et al., 2019). In birds, THs regulate metabolic rate and thermoregulation (Krishnan et al., 2023), suggesting that they may influence heat transfer to eggs via parental heat production and potentially affect egg-turning activity. Moreover, environmental PFAS contamination has been linked to TH levels in birds. For example, PFOS and PFCAs have been found to be positively correlated with triiodothyronine (T3) and thyroxine (T4) hormones in black-legged kittiwakes (Ask et al., 2021). In great black-backed gull (*Larus marinus*), PFOS, PFUnA, PFDoDA, PFTriA, and PFTeDA were positively associated, whereas PFHxS showed a negative relationship (Sebastiano et al., 2021). Inspired by the knowledge gap between THs and nest attendance, and the limited research connecting PFAS to behaviour, we first examined associations between PFAS contamination and THs, and then investigated how nest attendance relates to both THs and PFAS in waterfowl.

Here, we studied two waterfowl species with contrasting breeding strategies: the cavity-nesting, income breeding common goldeneye (hereafter, goldeneye) and the ground-nesting, capital-breeding common eider (hereafter, eider). The contrasting breeding habitats, feeding behaviour during incubation and diets of the two study species likely results in different patterns of internal contaminant processing and in blood circulation, making them valuable models for comparing the PFAS associations with physiology and behaviour.

To explore the potential species-specific differences in ecology that might influence nest attendance, we first compared mean attendance between species. We expected that cavity nesting would provide goldeneye with greater thermal buffering compared to the eiders. Then, based on the hypothesis that PFAS can disrupt THs regulation, we evaluated correlations between PFAS concentrations and circulating THs across species. We hypothesized that PFAS contamination—both total exposure and individual compound concentrations—may be linked to altered nest attendance via endocrine and/or other physiological pathways, including associations with circulating THs and, potentially, other indicators of physiological stress. Thus, we evaluated the contribution of PFAS concentrations and THs in explaining variation in nest attendance. Finally, because hatching success integrates multiple ecological and physiological determinants and prior studies report mixed associations with PFAS exposure, we tested whether PFAS contamination was associated with hatching success in either species.

2. Materials and methods

2.1. Study species and populations

Goldeneyes breed near freshwater lakes, whereas eiders are sea ducks, in Finland inhabiting the archipelago in the Baltic Sea. Both species display exclusive female-only care and produce precocial young (Milonoff et al., 2002; Öst et al., 2003), but distinctly differ in their breeding ecology. Goldeneyes are income breeders, feeding on aquatic invertebrates throughout the incubation period.

In contrast, eiders largely rely on stored energy reserves, which may may be accumulated both on the wintering grounds and at the breeding sites (Jaatinen et al., 2016). They feed mainly on marine invertebrates, particularly blue mussels (*Mytilus spp.*), and during incubation typically leave the nest only to drink (Criscuolo et al., 2000; Hellman, 2017). From 28 April to 22 June 2022, we monitored 20 nestboxes of a breeding population of common goldeneye in Maaninka, NorthSavo region, Finland (63°6′ N, 27°9′ E). The breeding area (~280 km^2) is characterized by a mosaic of coniferous forests, small lakes and ponds, and four larger lakes. Most shorelines are adjacent to farmland and summer cottages. We did not observe any nest predation by pine marten (*Martes martes*), the main goldeneye predator in Finland (Pöysä et al., 2025). In 2023 (26 April- 2 July), we monitored two colonies of an eider population in southwest, Finland. Bengtskär (59°44′N, 22°30′E), is a rocky lighthouse island (about 2 ha), approximately 25 km from the mainland. Since 1995, it has been inhabited during the breeding season due to its operation as a museum, which also serves as a deterrent to predators, particularly the white-tailed eagle (*Haliaeetus albicilla*). The second site, almost 30 km away (Fig. 1), is Tvärminne archipelago (59°50′N, 23°15′E), consisting of 14 small islands with a total area of approximately 15 km^2 (monitored islands: approximately 1.04, 1.79 and 8.55 ha) located near a research station. This colony has experienced high predation pressure by white-tailed eagle during the past decades (Öst et al., 2022), resulting in lower hatching success rate (Bengtskär: 71.4% of 35 nests in 2023, Tvärminne: 52.8% of 214 nests across all 14 islands). In total, 39 eider nests were monitored (25 at Bengtskär; 14 across three islands in Tvärminne). Eight nests in Tvärminne and one in Bengtskär were deserted by females. Due to these nests abandonments and insufficient amount of behavioural data for some nests, sample size varies across analyses.

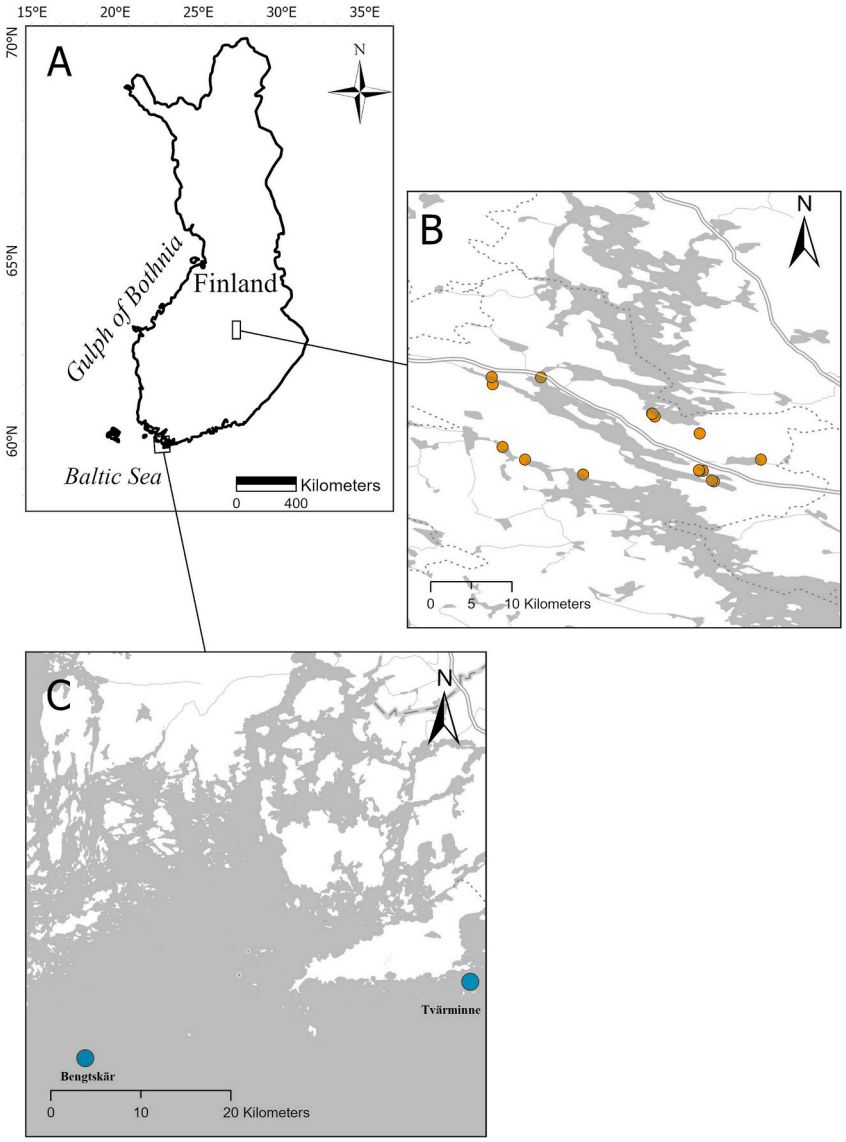

Fig. 1. Map of the study areas by species. Gold points (panel B) indicate goldeneye nestboxes (n = 20) at Maaninka. Blue points (panel C) represent eiders at Bengtskär (n = 25) and on the three islands in Tvärminne (n = 14).

2.2. Behavioural monitoring

We deployed data loggers equipped with a temperature thermistor, triaxial accelerometer and magnetometer, enclosed within 3D printed artificial eggs (Shaffer et al., 2014). The artificial eggs were designed to match the natural size and shape of each species' eggs and were filled with beeswax to match egg mass (eider: 100 g, goldeneye: 60 g). The sensors recorded internal temperature (i.e., core egg temperature, every 1 s) and angular change (1-2°) across three axes (roll, pitch, yaw) (Fig. S1). Egg orientation was estimated from accelerometer data (gravity and three-axis motion) combined with magnetometer data (Earth's magnetic field). Raw sensor data were stored on 4 GB microSD cards during deployment. For most birds (except for one goldeneye and one eider), the artificial egg was placed in the nest in the first half of incubation to maximize recording duration (Table S1). Egg placement in a nest was always done by one person. Conspecific brood parasitism is common in both species (Pöysä et al., 2001; Waldeck et al., 2004), meaning that they accept eggs laid by other females in their nest. Natural clutch size averages 8.30 ± 2.00 eggs (mean ± SD) in goldeneye (Milonoff et al., 2004) and 4.60 ± 0.10 eggs (mean ± SD) in eiders (Öst et al., 2022), and the artificial eggs were added to existing clutches (before adding the artificial egg: goldeneye: 10.0 ± 3.50; eider: 4.40 ± 1.20, mean ± SD). Additionally, because the two species were sampled in different years, we measured ambient temperature to assess potential differences between fieldwork periods and for possible correlations with egg turning and egg temperature. Ambient temperature was recorded using iButton DS1921 loggers, placed beneath the nestboxes for goldeneyes (n = 17) and approximately 1 m from the nest for eiders (n = 27).

Due to logger battery failures (3 out of 20 in goldeneye; 5 out of 37 in eider), or insufficient data due to early nest abandonment (4 eiders), the number of useable behavioural recordings were lower than the number of deployed devices. In total, we obtained egg-turning and temperature data from 17 goldeneyes and 28 eiders (25 from Bengtskär; 3 from Tvärminne), and Tables S2 and S3 show recorded nest attendance in both species. Loggers' data were trimmed by removing the first 2 h, the last 30 min, and the period corresponding to blood sampling disturbance to account for our time in the colony and the delay in female return to the nest.

2.3. Egg logger processing

The raw data for each logger were first processed in MATLAB (The MathWorks, Inc., 2020) using a purpose-built script developed by Shaffer et al. (2014). In brief, the script combined accelerometer data (gravity and motion) and magnetometer data (Earth's magnetic field) to compute Euler angles, representing orientation as yaw (orientation about the vertical axis), pitch (orientation about the lateral axis), and roll (orientation about the longitudinal axis). From these Euler angles, the shortest angular change between consecutive time points was calculated, resulting in a single scalar value, representing the egg's total rotation over each 1 s interval. These angular changes, along with corresponding temperature measurements, were extracted from the processed data. Subsequent data cleaning, analysis, and plotting were conducted in R (version 4.4.0; R Core Team, 2024). A turning event was defined using a threshold of 10°— a turn started when the angular change exceeded 10°, continued while it remained above this threshold, and ended when it dropped below 10°. The next turn began the next time the threshold was crossed. This allowed us to calculate the start, end, duration, and angle change of each turning event as well as duration between consecutive turning events and the proportion of time the egg was stationary across a given period (e.g., hour). Variables defined as indicators of nest attendance included: hourly average egg-turning frequency (the total number of turning events divided by the overall recorded hours); hourly average egg temperature (mean egg temperature across all recorded hours), total daily egg-turning rates (total counts of turns per recorded incubation day) and average daily egg temperature (averaged egg temperature per recorded incubation day).

2.4. Blood sampling

To minimize the risk of nest abandonment, we aimed to collect blood samples during the late stage of incubation. However, due to fieldwork logistics in Tvärminne, birds were sampled on the same occasion as the deployment of the artificial egg. Consequently, one Tvärminne female was sampled on the first day of incubation, and she unfortunately abandoned the nest after ~3.4 days (Table S1).

Approximately 2-3 mL of blood was collected from the incubating females from the brachial vein and transported on cold elements to a field laboratory for centrifugation. Plasma was separated and stored in individual Eppendorf tubes for PFAS and THs analyses, stored at −20 °C during fieldwork, and transferred to −80 °C upon arrival to the University of Turku. Females were also measured for body mass (to the nearest 1 g) and maximum wing length — from the bent carpal joint to the tip of the longest primary feather (to the nearest 1 mm). Body condition index was calculated as the standardized residuals from a linear regression of log-transformed body mass as a function of log-transformed wing length (Öst and Steele, 2010).

Blood samples for PFAS and hormone analyses were collected from a total of 18 goldeneyes and 37 eiders (23 from Bengtskär and 14 from Tvärminne). All sampled individuals (18 goldeneyes and 37 eiders) were included in testing correlations between PFAS and THs. Among individuals for which both blood and behavioural data were available, the final dataset included 15 goldeneyes and 26 eiders (23 from Bengtskär and 3 from Tvärminne). The handling procedure was approved by the Animal Experiment Board at the State Provincial Office of Southern Finland and the Finnish Wildlife Agency under the permit numbers **ESAVI/15854/2022** and **2023-5-000–30296–4**. Access to the Maaninka nestboxes was provided by landowners, and access to the islands were granted by Bengtskär Oy and Tvärminne Zoological Station.

2.5. Hatching success

For goldeneyes, we estimated hatching date in nests by egg flotation during the blood sampling visit. Eggs were floated in lukewarm water because buoyancy increases as incubation progresses (air cell enlarges and egg density decreases). Incubation stage and time to hatching were inferred from egg vertical position and floatation angle (Liebezeit et al., 2007). Accordingly, we visited nestboxes on the expected hatching date, and the number of ducklings per nest was counted. Hatching success was calculated as the proportion of hatched eggs per the original clutch size. For eiders with artificial eggs and with useable logger data, hatching date was determined via egg floating for some nests (Bengtskär: n = 11; Tvärminne: n = 3) during the blood sampling. In other eider nests (Bengtskär: n = 12), the floatation test could not be performed due to time constraints during the sampling. In these cases, when logger data covered the end of incubation (n = 5), a sudden continuous drop in egg temperature identified the end of incubation. When logger data did not extend to the end of incubation, we estimated the initiation date of incubation from lighthouse staff observation of newly initiated nests, and hatching date was calculated accordingly. Laying date estimated via egg floatation in eiders have been shown not to differ significantly from those based on direct observation of actual laying (Kilpi and Lindström, 1997).

In Bengtskär, restricted access due to weather and boat schedule prevented visits on the exact hatching date for most nests. Thus, nest remains were collected, and the number of hatched eggs was estimated by counting eggshell remains (Öst and Steele, 2010).

2.6. PFAS analysis

Plasma samples were transported on dry ice to the Norwegian University of Science and Technology (NTNU) for PFAS analyses. The PFAS

extraction procedure followed a method described by Trimmel et al. (2021) with minor modifications, as detailed in the Supplementary Materials, section PFAS analysis. The solid-phase extraction (SPE) was performed using Hybrid-SPE®-Phospholipid cartridges (Supelco, Bed wt. 30 mg, 1 mL) and the eluate was analysed using ultraperformance liquid chromatography tandem mass spectrometry (UPLC/MS/MS). Standard reference material, reagent blanks, spiked samples and quality control spike samples were included in each batch of samples. Recovery tests and full method description can be found in the Supplementary Materials, Section PFAS analysis. Table S4 shows the limits of detection (LOD) and limits of quantification (LOQ) for the detected compounds.

A total of forty-one compounds were targeted in goldeneyes and twenty-five compounds in eiders. The difference reflects an update to the target compound list by the laboratory between the two analysis years. For statistical analyses, we used the sum of all detected compounds (∑PFAS) to represent total PFAS contamination, and compounds detected in over 60% of samples are hereafter referred to as major compounds. For major compounds, concentrations below the LOD were replaced with ½ LOD (Antweiler and Taylor, 2008). Values between LOD and LOQ were retained as measured.

2.7. Thyroid hormone analysis

Total thyroxine (T4) and triiodothyronine (T3), the biologically active form of T4 (Darras, 2022), were analysed at the University of Turku and Åbo Akademi University, Finland. The extraction protocol is described by Ruuskanen et al. (2016), followed by a nano-LC/MS/MS protocol of measurement (Hsu et al., 2022; Ruuskanen et al., 2018). $A^{13}C_{12}$-T4 reference standard was used for recovery correction, while $^{13}C_6$-T3 and $^{13}C_6$-T4 served as internal standards for T3 and T4, respectively. The LOD and the corresponding LOQ are shown in Table S5 (Ruuskanen et al., 2018).

2.8. Statistical analysis

We first compared nest attendance patterns (hourly egg-turning frequency and hourly average egg temperature) between species using unpaired two-sample Welch's *t*-test. This comparison provided insight into potential species-specific differences in nest attendance that could influence associations with PFAS and THs. Similarly, we compared average hourly ambient temperatures recorded by the iButton temperature loggers between the two species. We then examined the relationships between ambient temperature and both egg-turning frequency and egg temperature using simple linear regression models (LMs), to assess whether ambient temperature could confound the observed associations with nest attendance.

Separately for each species, we used daily nest attendance values per individual to test whether egg-turning (counts per day), and egg temperature (daily average) were significantly associated with incubation stage (days since incubation onset). This step provided species-specific insight into whether incubation stage had a systematic influence on nest attendance and whether variation in the incubation period by the loggers – resulting from differences in the number of days recorded — should be considered in subsequent analyses of relationships between nest attendance, PFAS, and THs. Model selection here and elsewhere, were performed using the *dredge* function from the MuMIn package (Bartoń, 2022) in R, which generates all possible subsets of models including all variables of interest. Models were ranked by Akaike's Information Criterion corrected for small sample size (AICc). When a single model had clear support (ΔAICc ≥2 to the next-best model), that top-ranked model was selected. When multiple models were similarly supported (ΔAICc <2), we selected the most parsimonious model among those within ΔAICc <2 of the top-ranked models (Symonds and Moussalli, 2011). We fitted generalized linear mixed models (GLMMs) with a negative binomial distribution for turning counts per day, and linear mixed models (LMMs) with a Gaussian distribution for daily temperature with female ID as random effect. We tested models with and without a random slope for incubation stage within female ID, allowing for individual-specific trajectories (Table S6). Model diagnostic of GLMMs were performed using the DHARMa package (Hartig and Lohse, 2022).

We also quantified the proportion of variance in nest attendance attributable to consistent inter-individual differences (after controlling for incubation stage; Table S7). For that, we calculated repeatability using the intra-class correlation coefficient (ICC), computed with the package rptR (Stoffel et al., 2017). This allowed us to assess how much of the possible correlations between average nest attendance and PFAS or THs may reflect stable behavioural difference among females. Because rptR package does not support negative binomial distributions, repeatability was estimated on the latent (log-link) scale, assuming Poisson variance (see Table S7 legend for further details). For interpretability, we used qualitative categories for repeatability (r): low (<0.3), moderate (0.3–0.5), and high (>0.5) (Bell et al., 2009).

In both species, daily egg temperature showed a strong link with incubation stage. Because females differed in the number of days with valid logger recordings (Table S2–S3), we controlled for the number of valid recording days per female as a covariate in models relating PFAS and THs to average hourly egg temperature. This variable accounted for inter-individual differences in logger data coverage (recording duration), which could otherwise bias estimates of average egg temperature.

To evaluate whether a relationship between THs (as response) and contamination with ∑PFAS (or separately, for individual major PFAS) occurred, we compiled data from both species to build LMs. We checked for PFAS associations with all THs: T3, T4 or T3:T4. Species differences were accounted for by adding an interaction term between PFAS and species. When this interaction was significant ($p < 0.05$), species-specific PFAS associations were examined using estimated marginal trends (emtrends) from estimated marginal means (EMMs) with the *emmeans* package in R (Lenth et al., 2025). When the interaction was not statistically significant but showed a trend ($0.05 < p < 0.1$), post hoc analyses were conducted in an exploratory manner to aid interpretation of potential species-specific patterns. Also, to test whether the association between body condition and our response variables differed between species, we included an interaction term between species and body condition during model selection. In addition, incubation stage (days since incubation onset at the time of blood sampling) was included as covariate (Table S8).

We used LMs to test the relationships between average nest attendance (response variable)—average hourly turning frequency and average hourly egg temperature— and PFAS contamination (total ∑PFAS and, separately, major individual compounds), as well as circulating T3 or T4 (in separate candidate models). Species was included as a fixed factor, along with a PFAS × species interaction term. Clutch size (goldeneye: range = 5-16; eider: 3-5 eggs) and incubation stage (days since incubation onset at the time of blood sampling) were also included as covariates in model selection. In model selection for egg temperature, we additionally included average egg-turning frequency as a fixed effect, given the hypothesis that turning influences temperature distribution during incubation. Further, because females differed in the amount of valid logger data available— and we observed a significant association between egg temperature and incubation stage (see above)— we accounted for this by including recording duration (number of valid recording days per female) as a covariate in model selection for egg temperature. Model diagnostics for LMs were performed using base R diagnostic plots. Multicollinearity among predictors in the final model was assessed using variance inflation factors (VIFs) with the *car* package in R, with VIF<3 considered indicative of low collinearity (Zuur et al., 2010). All explanatory variables in LMs were centred and scaled. Table S8 shows all the selected models and table A1 shows the associated statistics.

Finally, we fitted a binomial GLM, to examine the association between hatching success and PFAS contamination. We tested PFAS

association with hatching success by comparing models with and without the potential contribution of egg temperature on hatching success. DHARMa residual diagnostics indicated significant overdispersion, which was further confirmed by calculating the sum of squared Pearson residuals divided by the residual degrees of freedom (dispersion parameter ~3.1). To account for overdispersion, we refitted the model using a quasibinomial error structure, which allows the variance to be estimated from the data.

We ran multiple models— with ∑PFAS and separately for each major PFAS compound— to test the associations between PFAS, THs and average nest attendance (response). Thereby, to minimize the risk of Type I error, we adjusted the p-values of interaction terms (between species and ∑PFAS or individual compounds) using the Benjamini–Hochberg false discovery rate (FDR) correction (Benjamini and Hochberg, 1995). We applied nonparametric bootstrapping with 5000 resamples to estimate the bias-corrected confidence intervals (CI) for model coefficients of species-specific significant associations, to assess the robustness of the direction and magnitude of the observed correlations (Westfall and Young, 1993) (Table S9).

3. Results

3.1. Nest attendance across species

Egg-turning frequency did not differ across species (goldeneye: 0.99 h^{-1}, eider: 0.92 h^{-1}; $t = 0.58$, $p = 0.57$). In contrast, goldeneye females maintained a significantly higher mean hourly egg temperature than eiders (Fig. 2B, $t = 2.51$, $p < 0.05$). Average hourly ambient temperature did not differ between species (goldeneye = 14.03 °C, eider = 12.3 °C; $t = 1.31$, $p > 0.05$) and was not associated with egg-turning frequency in either species (both $p > 0.05$). Ambient temperature was positively correlated with egg temperature in goldeyes only ($p < 0.05$, Fig. S2).

3.2. Nest attendance in relation to incubation stage

In goldeneyes, incubation stage showed a weak association with daily turning counts (non-significant in the model including random slope), but it was strongly related to average daily egg temperature (GLM; $p < 0.001$, Table S6). Model predictions indicated an increase of ~3 °C from day 1 to day 30 of incubation. In eiders, incubation stage did not correlate with daily turning counts, but it had a significant relationship with average daily egg temperature (GLM; $p < 0.001$, Table S6). Model prediction indicated an increase of ~6.30 °C from day 1 to day 26 of incubation. These results justify our choice to include incubation stage, in models linking average egg temperature with PFAS and T3.

3.3. Nest attendance repeatability

After controlling for incubation stage, a high proportion of variance was attributed to consistent among-female differences in goldeneyes for both daily egg-turning (Table S7; ICC = 0.88, 95% CI = 0.73-0.93) and daily egg temperature (ICC = 0.72, 95% CI = 0.51-0.83). Incubation stage explained little overall variance in daily egg-turning (marginal R^2 = 0.002, conditional R^2 = 0.48), while accounting for a modest proportion of variance in daily egg temperature (marginal R^2 = 0.11, conditional R^2 = 0.75). Similarly, in eiders, daily turning rates showed moderate among-individual consistency (Table S7; ICC = 0.41, 95% CI = 0.20-0.54), with negligible overall variance explained by incubation day (marginal R^2 = 0.000, conditional R^2 = 0.090). Average daily egg temperature in eiders exhibited lower among individual consistency (ICC = 0.30, 95% CI = 0.14-0.45), while incubation day accounted for a moderate proportion of total variance (Table S7; marginal R^2 = 0.14, conditional R^2 = 0.40). Together with the results on nest attendance across incubation days, these results indicate that egg-turning is primarily structured by stable individual differences, whereas egg temperature reflects both consistent among-female differences and temporal changes across incubation.

3.4. PFAS and THs

A total of nine PFAS compounds were detected in the plasma of goldeneyes (N = 18), of which four compounds were detected in over 60% of samples (major compounds): PFOS, PFUnA, PFNA, and PFDoDA. In eiders (N = 37), fourteen PFAS compounds were detected with four major compounds: PFOS, PFNA, PFHxS, and PFUnA. Major compounds, ranked by mean detected concentration from highest to lowest, along with T3 (goldeneyes:18, eiders:34) and T4 levels (goldeneyes:18, eiders; 35) are shown in Table 1.

At the interspecific level, T3 levels did not differ significantly between eiders and goldeneyes (Wilcoxon rank-sum test: W = 407, p = 0.052). Eiders had significantly higher T4 than goldeneyes (W = 447, p = 0.012; Table 1). Species did not differ in T3:T4 from each other ($p > 0.05$). Linear models revealed no significant interactions between species and ∑PFAS or individual PFAS compounds in relation to THs after p-value correction (all adjusted $p > 0.05$; Table A1).

3.5. Egg-turning, PFAS and THs

After adjusting for multiple comparisons, there was only weak evidence for interactions between PFAS (∑PFAS, PFOS and PFUnA) and species in relation to egg turning (all adjusted p = 0.077). Nevertheless, exploratory analyses using estimated marginal trends suggested positive correlations between ∑PFAS, PFOS and PFUnA and egg-turning,

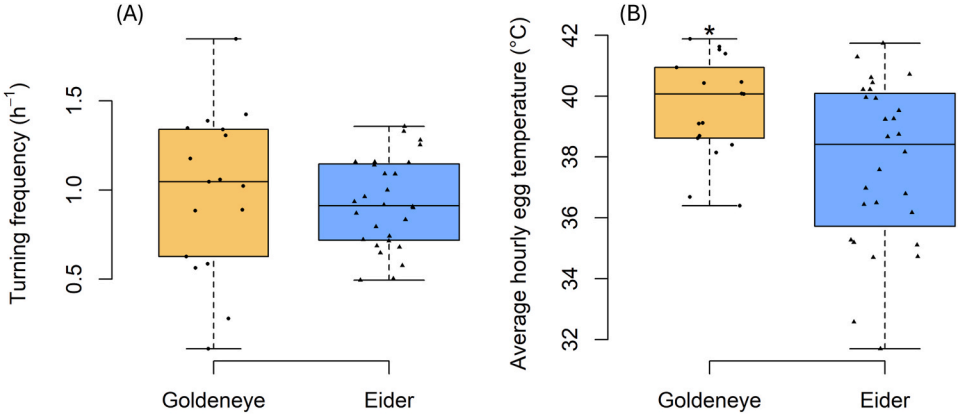

Fig. 2. (A) Egg-turning frequency did not differ significantly between species. (B) Female goldeneyes (N = 17) maintained higher hourly average egg temperature (°C) than female eiders (N = 28). Dots represent goldeneye data and triangles represent eider data.

Table 1
Sum of all PFAS compounds detected in at least one sample (∑PFAS: 9 compounds in goldeneyes,14 compounds in eiders), and individual major PFAS compounds detected in more than 60% of samples. Also shown are T3 and T4 concentrations in common goldeneye (N = 18) and in common eider (PFAS: N = 37, T3: N = 34, T4: N = 35).

Species	PFAS (ng/g plasma); THs (pg/μl)	range	mean ± SD
Common goldeneye	$\sum_9$ PFAS	2.56-45.1	17.4 ± 13.2
	PFOS	0.54-20.9	7.83 ± 6.28
	PFUnA	0.04-16.9	4.26 ± 4.50
	PFNA	0.22-12.3	2.70 ± 2.83
	PFDoDA	0.02-1.96	0.73 ± 0.60
	T4	10.1-51.8	23.2 ± 10.7
	T3	0.47-6.33	1.66 ± 1.43
Common eider	$\sum_{14}$ PFAS	2.94-32.3	16.2 ± 8.67
	PFOS	0.45-14.6	6.82 ± 3.70
	PFNA	0.22-13.7	4.80 ± 3.60
	PFHxS	0.22-4.80	1.86 ± 1.11
	PFUnA	0.04-2.05	0.67 ± 0.62
	T4	13.9-63.8	32.1 ± 13.2
	T3	0.36-4.60	2.17 ± 1.21

observed only in the goldeneye (Table A1; Fig. 3A). The PFUnA slope was less robust (Fig. 3B), as the 95% bootstrap percentile confidence interval included zero (Table S9), indicating weaker evidence for a positive association between PFUnA and goldeneye egg-turning compared with ∑PFAS and PFOS.

3.6. Egg temperature, PFAS, and hatching success

Following adjustment for multiple comparisons, the ∑PFAS × species interaction was not significant in relation to egg temperature (Table A1; adjusted p = 0.172), despite visually apparent opposite trends between species (Fig. 4A). However, a significant PFOS × species interaction existed (adjusted p < 0.05; Table A1). Post hoc analyses using emtrends showed that in eiders, higher PFOS concentrations were significantly associated with lower average egg temperature (Fig. 4B; p < 0.001), whereas in goldeneyes, the slope estimate was numerically negative, but not statistically different from zero (Fig. 4B; p > 0.05). The GLM for hatching success, using a quasibinomial error structure to account for over dispersion, did not detect any significant association between hatching success and PFAS contamination. Excluding PFAS from the model, average egg temperature was positively associated with hatching success across the combined dataset (p < 0.05; Table A1; Fig. S3).

4. Discussion

4.1. Species differences in nest attendance

The relatively low egg-turning frequencies in our study species (goldeneye: 0.990 h^{-1}, eider: 0.920 h^{-1}) align with the predictions for precocial species with long incubation period and low egg albumin content. In such species, embryos rely more heavily on yolk resources, making them less dependent on frequent egg-turning (Deeming, 2009). Using the same type of loggers, higher egg-turning frequencies have been reported in several seabird species with less precocial developmental modes, including approximately 2 h^{-1} in Cassin's auklet (*Ptychoramphus aleuticus*; Kelsey et al., 2016), Western gull (*Larus occidentalis*) and Laysan albatrosses (*Phoebastria immutabilis*; Shaffer et al., 2014) and 3.08 h^{-1} in Förster's tern (*Sterna forsteri*; Taylor et al., 2018). Polar petrel species with long development times have lower turning rates of ~1.3 h-1 (Shaffer et al., 2021), suggesting phylogenetics and environment have a significant effect on egg attendance patterns.

Differences in mean egg-temperature between the two study species may reflect their different breeding strategies. Income-breeding goldeneyes require frequent incubation recesses to forage, and the thermal buffering of nestboxes likely minimizes the cooling associated with these absences. In contrast, capital-breeding eiders undergo prolonged fasting throughout incubation, and several studies suggest that extended food deprivation can induce a down-regulation of body temperature in birds. This fasting-related reduction in body temperature may, in turn, influence egg temperature. However, evidence for fasting-induced hypothermia is limited in waterfowl and most empirical support comes from studies on smaller birds (McKechnie and Lovegrove, 2002; Laurila et al.,

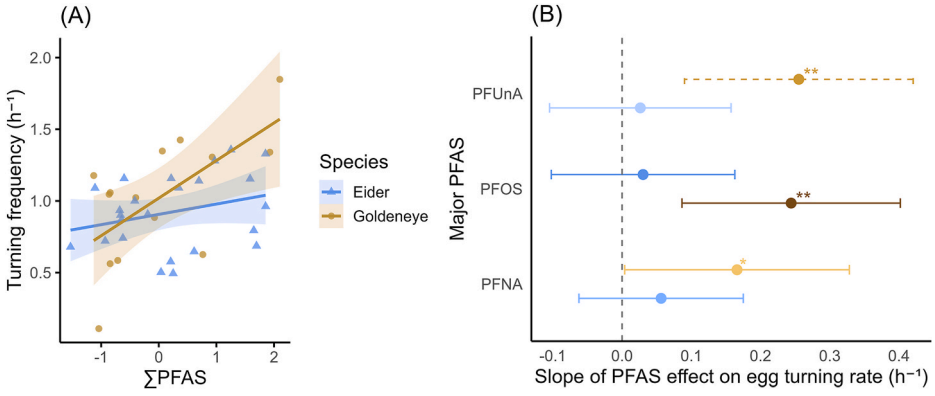

Fig. 3. (A) Exploratory analysis using estimated marginal trends suggested species-specific relationships between ∑PFAS concentrations and average hourly egg-turning frequency. A positive association was observed in goldeneye females (post hoc slope p < 0.01), whereas no meaningful association was detected in eiders. Points and triangles represent goldeneye and eider data, respectively. Lines and shaded areas show species-specific linear regressions (light brown for goldeneyes, light blue for eiders) and 95% confidence intervals. PFAS values were scaled. (B) Exploratory analyses suggested that among major individual PFAS detected in both species, PFOS had a positive association with egg-turning frequency in goldeneyes (post hoc slope p < 0.01). The PFUnA regression slope is dashed because its 95% bootstrap confidence interval included zero. Darker colors indicate higher compound concentrations (brown gradient for goldeneyes, blue gradient for eiders). The dotted black line represents a slope of zero (no association).

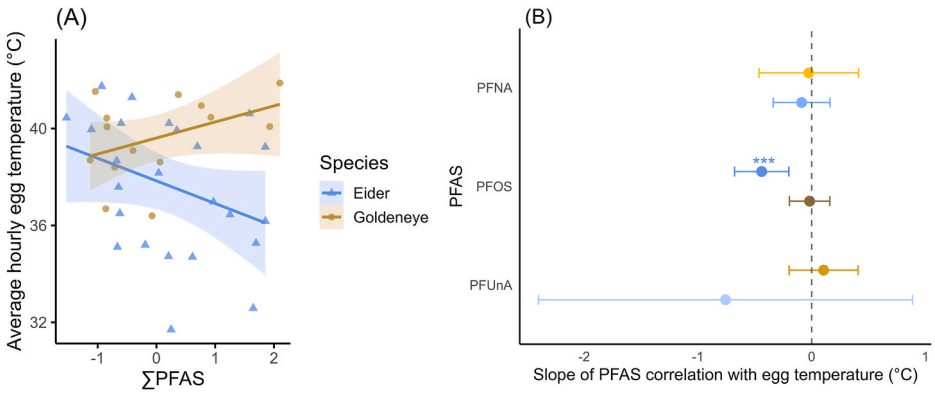

Fig. 4. (A) Exploratory visualization of species-specific relationships between ∑PFAS concentrations and average hourly egg temperature. Points and triangles represent goldeneye and eider data, respectively. Lines show species-specific linear regressions with shaded 95% confidence intervals (light brown for goldeneyes, light blue for eiders). PFAS concentrations were scaled. (B) Among major individual PFAS, detected in both species, the PFOS × species interaction was significant, indicating that the relationship between PFOS and egg temperature differed between species. Post hoc comparison showed a significant negative relationship between PFOS and average hourly egg temperature in eiders. Dotted black line represents zero (no association), and compounds with higher concentrations are shown in darker colors (brown gradient for goldeneyes, blue gradient for eiders).

2005). Nonetheless, facultative hypothermia has been documented in some larger species under energetic constraints; for example, barnacle geese (*Branta leucopsis*) reduce body temperature during autumn migration to slow down rates of fat depletion (Butler and Woakes, 2001). Thus, more research is needed to explore whether a similar energy-conserving mechanism might operate in fasting eiders during incubation. A potential limitation of our study is that the two species were sampled in different years. However, average ambient temperature did not differ between study periods, suggesting that differences in ambient temperature are unlikely to explain the observed species-specific differences in egg temperature.

Parental investment theory predicts higher investment as the value of the current brood rises, as is the case with advancing incubation (e.g., Verboven and Tinbergen, 2002; Ackerman and Eadie, 2003). For instance, female eiders are less likely to desert a nest with late-stage embryos (Bourgeon et al., 2006). In our data, however, we observed that goldeneye daily turning counts showed a weak association (yet significant) with incubation stage, whereas no association existed in eiders (Table S6). This suggests that egg-turning may be less tightly linked to systematic temporal parental investment than other components of incubation behaviour. At the same time, goldeneyes exhibited high repeatability in egg-turning, indicating that turning behaviour is strongly influenced by stable individual differences. In contrast, eiders showed only moderate egg-turning repeatability (ICC = 0.41), suggesting among-individual consistency alongside substantial within-individual variation. This is consistent with previous findings, showing that the duration of incubation recesses is unrelated to incubation stage in female eiders (Bolduc and Guillemette, 2003), and with recent camera-trap evidence that eider recess patterns are strongly shaped by site-specific predation risk and diel activity (Ilvonen, 2025). Thus, in goldeneyes where egg-turning appears to be a highly consistent individual trait, associations with individual-level PFAS contaminations are more likely to be detectable. In eiders, greater within-individual variability in turning behaviour may obscure minimal PFAS associations with egg-turning.

4.2. Nest attendance and PFAS contamination

Before discussing PFAS-nest attendance associations, we briefly compare the PFAS concentrations in our study with those reported for other waterbirds. Plasma PFAS concentrations in the current study were within the range reported for other waterbirds and seabirds in northern regions (Sun et al., 2023). For instance, PFOS levels in goldeneyes (7.83 ± 6.28 ng/g plasma, mean ± SD) and eiders (6.82 ± 3.70 ng/g plasma, mean ± SD) were comparable to those reported in black-legged kittiwakes from Svalbard (mean 7.32 ng/mL in plasma; Ask et al., 2021), noticing that ng/g and ng/mL are approximately comparable for plasma.

The suggestive positive association between egg-turning and PFAS in goldeneyes, based on exploratory analyses, aligns with findings by Blevin et al. (2020), who reported positive relationships between PFOS and PFCAs and egg-turning in black-legged kittiwakes, an income-breeding seabird. In our study, PFOS was the dominant PFAS in both goldeneyes and eiders, and although the PFAS × species interactions were not statistically significant (∑PFAS × species and PFOS × species, adjusted $p = 0.077$), exploratory post hoc analyses suggested a potential positive relationship between ∑PFAS, PFOS, and egg-turning in goldeneyes. This trend may reflect behavioural responses to PFAS-associated stress, although this interpretation remains speculative. For instance, if PFAS exposure is associated with physiological stress that shortens female incubation bouts, she may turn eggs more frequently to compensate for reduced time spent on the eggs. Blevin et al. (2020) also suggested a potential link between PFAS and prolactin stimulation, which could be related to higher egg-turning. In our study, we found no significant associations between PFAS concentrations and THs. The physiological mechanisms underlying PFAS—egg-turning associations warrant further investigation.

Higher PFOS concentrations in our study were significantly associated with lower average egg temperature, only in eiders. Notably, egg-turning was positively associated with egg temperature in eiders (Fig. S4), yet the PFAS-egg-turning relationships in eiders were not statistically significant (despite a numerically positive slope). This suggests that the negative PFOS–egg temperature association is unlikely to be attributable to reduced egg-turning and may instead reflect other incubation behaviours or PFAS-related links with thermoregulation in fasting females. Importantly, ambient temperature was not significantly associated with egg temperature in eiders (Fig. S2), suggesting that the observed PFOS-egg temperature correlation is unlikely to be confounded by ambient temperature. One possibility is that goldeneye eggs maintain a higher baseline temperature, providing a larger buffer against PFAS-related temperature drop, whereas in eiders, lower baseline egg temperature makes them more sensitive to small changes associated with PFAS. Supporting this idea, an experiment on wood duck (*Aix sponsa*) has shown that even small differences in incubation temperature (<1 °C) can influence stress responsiveness in hatchlings (DuRant, 2011). This suggests that baseline differences in egg temperature across species may underline species-specific sensitivity to PFAS. Because egg temperature is a key determinant of embryonic development, even slight but

prolonged reductions may influence incubation outcomes. Therefore, lower egg temperature associated with higher PFOS concentrations could have downstream consequences for embryo development, although this would need to be tested experimentally.

Eiders showed substantially lower repeatability in egg temperature (ICC = 0.30), with incubation stage contributing a relatively larger share of the observed variance (Marginal $R^2 = 0.14$). Lower repeatability and stronger variation in egg temperatures in common eiders may reflect the greater sensitivity of ground nests to fluctuating nest microclimates. In common eiders, nest shelter can improve thermal conditions and reduce incubation costs, whereas exposed nests experience greater heat loss and faster mass loss during incubation (D'Alba et al., 2011). Such environmentally driven variation, partly outside the female's control, could increase temporal variability in egg temperature and potentially make any relationship with PFAS easier to detect if PFAS exposure is associated with reduced capacity to buffer eggs against thermal challenges.

The negative PFOS-egg temperature association in eiders was partly complicated by the positive relationship between PFOS concentration and recording duration (Fig. S5). Because recording duration is associated with the incubation stage covered by the logger data, it may partly reflect breeding phenology. In Baltic common eiders, breeding phenology is linked to state-dependent shifts in the relative use of stored versus locally acquired resources (e.g., early-breeding heavy females relying more on stored reserves and shifting toward local resources later in the season (Jaatinen et al., 2016), which could in turn generate phenology-related differences in contaminant exposure or the geographic origin of exposure (wintering vs breeding grounds). Importantly, however, the negative PFOS-egg temperature association persisted after controlling for recording duration, suggesting that uneven sampling duration is unlikely to fully account for the observed relationship. Future studies could explicitly account for individual breeding phenology and use tracers of resource origin alongside direct measurements of incubation recess behaviour to separate phenology-related exposure differences from behavioural versus physiological effects on egg temperature.

4.3. Circulating thyroid hormones in relation to PFAS and nest attendance

Eiders exhibited higher circulating T4 levels than goldeneyes, while T3 levels were slightly higher but did not differ significantly between species. We found no significant species differences in the relationship between PFAS and either T4 or T3. Similarly, neither T3 nor T4 appeared to influence nest attendance in our dataset. Consequently, we cannot infer that PFAS associations with nest attendance reflect variation in thyroid hormone levels. Overall, evidence for PFAS and THs relationships in birds is mixed: positive associations have been found between linPFOS and C9-C14-PFCA and T4 and T3 in kittiwakes (Ask et al., 2021), as well as between several PFAS and T3 in great black-backed gulls (Sebastiano et al., 2021). In contrast, studies on herring gull chicks (*Larus argentatus*) reported inconsistent associations for perfluorodecanoic acid (PFDA), PFDoDA, and PFTeDA (Sebastiano et al., 2023), while a negative relationship between PFHxDA and T3:T4 has been documented in peregrine falcon nestlings (Sun et al., 2021). Given these inconsistencies across species and compounds, controlled experimental studies are needed to clarify how PFAS exposure influences thyroid function and its potential links with nest attendance in birds.

4.4. Hatching success and PFAS

No significant association was found between PFAS and hatching success. Overall, the literature on PFAS effects on hatching success remains inconsistent. For instance, PFOS concentrations in eggs were significantly associated with lower hatching success in tree swallow (*Tachycineta bicolor*) (Custer et al., 2014), while experimental exposure to a mixture of PFOS:PFHxS via drinking water increased hatchability in Northern bobwhite (*Colinus virginianus*) (Dennis et al., 2020). No significant PFAS-hatching success associations were observed in great tits (*Parus major*) or blue tits (*Cyanistes caeruleus*) (Groffen et al., 2024), nor in another study on tree swallow (*Tachycineta bicolor*) (Custer et al., 2019). It is also important to acknowledge the challenges in comparing field results with experimental studies. In wild birds, potential PFAS associations with reproductive output should be considered not only in the context of biological variation, but also relative to other environmental stressors, concurrent chemical exposures, and potential adaptation to pollution (Custer, 2021).

We acknowledge that the hatching-success model may have limited statistical power to detect subtle correlations with PFAS concentrations. In addition, hatching success estimates for some birds at Bengtskär may have higher uncertainty (see methods), which could further reduce our ability to detect such associations. Other environmental stressors may mask any potential effect of PFAS on hatching success. For instance, high nest predation risk in Tvärminne eiders (Öst et al., 2022), and conspecific brood parasitism—prevalent in dense eider colonies (Waldeck et al., 2004), such as Bengtskär (230 nests/ha in 2023) and also common in our goldeneye population (Vakili et al., 2025)—can strongly influence hatchability and may obscure any PFAS– hatching success association. Our limitations to control for these factors and the inconsistencies in PFAS-hatching success literature, highlight the need for experimental studies that can directly test the effects of PFAS and evaluate underlying mechanisms, including potential endocrine disruption.

5. Conclusion

This study provided insights into the relationship between PFAS contamination and nest attendance in waterfowl species with different breeding strategies. Our results suggested some species differences in nest attendance, which may contribute to the observed species-specific patterns in PFAS associations, particularly in relation to egg temperature. We found no evidence that thyroid hormone levels were related to the observed associations between PFAS and nest attendance.

Given the correlative nature of this study, and the potential for limited power and unmeasured ecological drivers to obscure effects, we refrain from drawing conclusion on PFAS mechanisms of action in relation with nest attendance. Therefore, future experimental studies using avian models could enhance our understanding of PFAS interactions with THs, and their potential consequences for nest attendance and egg hatchability. Such studies would also allow embryonic stages to be controlled for when testing how PFAS exposure is associated with incubation behaviour.

CRediT authorship contribution statement

Farshad S. Vakili: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Scott A. Shaffer:** Writing – review & editing, Validation, Software, Resources, Methodology. **Veerle L.B. Jaspers:** Writing – review & editing, Resources, Methodology. **Silje Peterson:** Writing – review & editing, Investigation. **Elise Lunde Steensland:** Writing – review & editing, Investigation. **Pentti Runko:** Writing – review & editing, Investigation. **Bertille Mohring:** Writing – review & editing, Investigation. **Markus Öst:** Writing – review & editing, Resources. **Kim Jaatinen:** Writing – review & editing, Resources. **Bin-Yan Hsu:** Writing – review & editing, Resources, Methodology. **Titiksha Peetumber:** Writing – review & editing, Investigation. **Nora M. Wilson:** Writing – review & editing, Resources. **Christian Sonne:** Writing – review & editing. **Stefan Björkman:** Writing – review & editing, Supervision. **Suvi Ruuskanen:** Writing – review & editing, Methodology. **Céline Arzel:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition.

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.

Acknowledgment

We would like to greatly thank our collaborators in the field and lab, Amalie V. Ask, Junjie Zhang, Alexandros Asimakopoulos, Ida Hermansson, Constance Woodman and the staff at Bengtskär. The work carried out by Farshad S. Vakili was funded by grants from Societas pro Funa et Flora Fennica, Finnish Foundation for Nature Conservation, Finnish Cultural Foundation (grant number 00241187 Central Fund), Finnish National Agency for Education. This study was carried out as part of the project DISRUPT funded by the Research Council of Finland (grant numbers: 333400 and 336261).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envres.2026.124643.

Table A1
Statistical summary of the selected models. When no significant association was found between the response variable and PFAS (neither ∑PFAS nor individual compounds), the model with the lowest AICc is presented. For example, for THs, the model including T4 as the response variable and PFNA and its interaction with species (PFNA × species; i.e., including main effects of PFNA and species, and their interaction term PFNA:species) as explanatory variables provided the best fit, although the PFNA × species interaction was not significant. Post hoc analyses were conducted using estimated marginal trends for significant ∑PFAS (or major PFAS) × species interactions, and were also explored for marginal interaction trends ($0.05 < p < 0.1$). P values are adjusted for multiple testing using false discovery rate (FDR) control (Benjamini and Hochberg, 1995). All independent variables are centred and scaled. An asterisk (*) indicates that the bootstrapped 95% confidence interval did not include zero.

Response	Independent variables	Estimate± SE	Test statistic	EMMs
T4 (pg/μl)	~ PFNA[1] × species[2] +Body condition[3] × species + Incubation stage[4]	8.14 ± 3.86 19.70 ± 5.02 5.69 ± 2.30	t = 2.10, **p = 0.16** t = 3.92, p < 0.001 t = 2.47, p = 0.018	_
Hourly average egg-turning frequency (h^{-1})	~ ∑PFAS × species	0.19 ± 0.10	t = 1.96, p = 0.077	Goldeneye~∑PFAS: 0.26 ± 0.08 (Estimate ± SE); t = 3.44, p = 0.002*
	~ PFOS × species	0.21 ± 0.10	t = 2.11, p = 0.077	Goldeneye ~ PFOS: 0.24 ± 0.08 (Estimate ± SE); t = 3.14, p = 0.003*
	~ PFUnA × species	0.23 ± 0.10	t = 2.20, p = 0.077	Goldeneye ~ PFUnA: 0.25 ± 0.08 (Estimate ± SE); t = 3.14, p = 0.003
Hourly average egg temperature (°C)	~ PFOS × species + Average hourly egg-turning frequency	0.42 ± 0.14 0.97 ± 0.36	t = 2.93, p = 0.024 t = 2.75, p = 0.009	Eider ~ PFOS: −0.44 ± 0.12 (Estimate ± SE); t = −3.75, p < 0.001*
Hatching success (proportion hatched)	~ Average hourly egg temperature	0.27 ± 0.11	t = 2.40, p = 0.021	_

[1] PFAS concentrations are in ng/g plasma.
[2] species: goldeneye and eider.
[3] Body condition: The standardized residuals from a linear regression of natural log-transformed body mass (g) as a function of natural log-transformed wing length (mm).
[4] days since incubation onset.

Data availability

The data used for this study is publicly available at Zenodo (https://doi.org/10.5281/zenodo.18547380). The R script is available on the first author's Github (https://github.com/FarshadSV/Artificial-eggs).

References

Ackerman, J.T., Eadie, J.McA., 2003. Current versus future reproduction: an experimental test of parental investment decisions using nest desertion by mallards (Anas platyrhynchos). Behav. Ecol. Sociobiol. 54, 264–273. https://doi.org/10.1007/s00265-003-0628-x.

Antweiler, R.C., Taylor, H.E., 2008. Evaluation of statistical treatments of left-censored environmental data using coincident Uncensored Data Sets: I. Summary statistics. Environ. Sci. Technol. 42, 3732–3738. https://doi.org/10.1021/es071301c.

Ask, A.V., Jenssen, B.M., Tartu, S., Angelier, F., Chastel, O., Gabrielsen, G.W., 2021. Per- and Polyfluoroalkyl substances are positively associated with thyroid hormones in an Arctic Seabird. Environ. Toxicol. Chem. 40, 820–831. https://doi.org/10.1002/etc.4978.

Banyoi, S.-M., Porseryd, T., Larsson, J., Grahn, M., Dinnétz, P., 2022. The effects of exposure to environmentally relevant PFAS concentrations for aquatic organisms at different consumer trophic levels: systematic review and meta-analyses. Environ. Pollut. 315, 120422. https://doi.org/10.1016/j.envpol.2022.120422.

Bartoń, K., 2022. MuMIn: Multi-Model Inference. R package version 1.46.0.

Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. Anim. Behav. 77, 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. Roy. Stat. Soc. B 57, 289–300.

Blevin, P., Shaffer, S.A., Bustamante, P., Angelier, F., Picard, B., Herzke, D., Moe, B., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2020. Contaminants, prolactin and parental care in an Arctic seabird: contrasted associations of perfluoroalkyl substances and organochlorine compounds with egg-turning behavior. Gen. Comp. Endocrinol. 291, 113420. https://doi.org/10.1016/j.ygcen.2020.113420.

Bolduc, F., Guillemette, M., 2003. Incubation constancy and mass loss in the Common Eider Somateria mollissima. Ibis 145, 329–332. https://doi.org/10.1046/j.1474-919X.2003.00143.x.

Bourgeon, S., Criscuolo, F., Bertile, F., Raclot, T., Gabrielsen, G.W., Massemin, S., 2006. Effects of clutch sizes and incubation stage on nest desertion in the female Common Eider Somateria mollissima nesting in the high Arctic. Polar Biol. 29, 358–363. https://doi.org/10.1007/s00300-005-0064-7.

Brown-Leung, J.M., Cannon, J.R., 2022. Neurotransmission targets of Per- and Polyfluoroalkyl Substance neurotoxicity: mechanisms and potential implications for adverse neurological outcomes. Chem. Res. Toxicol. 35, 1312–1333. https://doi.org/10.1021/acs.chemrestox.2c00072.

Buck, R.C., Franklin, J., Berger, U., Conder, J.M., Cousins, I.T., de Voogt, P., Jensen, A.A., Kannan, K., Mabury, S.A., van Leeuwen, S.P.J., 2011. Perfluoroalkyl and polyfluoroalkyl substances in the environment: terminology, classification, and origins. Integr Environ Assess Manag 7, 513–541. https://doi.org/10.1002/ieam.258.

Bursian, S.J., Link, J.E., McCarty, M., Harr, K., Roberts, J., Simcik, M.F., 2021. Dietary exposure of Japanese quail (Coturnix japonica) to perfluorooctane sulfonate (PFOS) and a legacy aqueous film-forming foam (AFFF) containing PFOS: effects on reproduction and chick survivability and growth. Environ. Toxicol. Chem. 40, 2521–2537. https://doi.org/10.1002/etc.5138.

Butler, P.J., Woakes, A.J., 2001. Seasonal hypothermia in a large migrating bird: saving energy for fat deposition? J. Exp. Biol. 204, 1361–1367. https://doi.org/10.1242/jeb.204.7.1361.

Byns, C., Lies, T., Thimo, G., Robin, L., Lieven, B., 2022. Bioaccumulation and trophic transfer of perfluorinated alkyl substances (PFAS) in marine biota from the Belgian North Sea: distribution and human health risk implications. Environ. Pollut. 311, 119907.

Costantini, D., Blévin, P., Herzke, D., Moe, B., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2019. Higher plasma oxidative damage and lower plasma antioxidant defences in an Arctic seabird exposed to longer perfluoroalkyl acids. Environ. Res. 168, 278–285. https://doi.org/10.1016/j.envres.2018.10.003.

Criscuolo, F., Gauthier-Clerc, M., Gabrielsen, G.W., Le Maho, Y., 2000. Recess behaviour of the incubating Common Eider Somateria mollissima. Polar Biol. 23, 571–574. https://doi.org/10.1007/s003000000123.

Custer, C.M., 2021. Linking field and laboratory studies: reproductive effects of perfluorinated substances on avian populations. Integrated Environ. Assess. Manag. 17, 690–696. https://doi.org/10.1002/ieam.4394.

Custer, C.M., Custer, T.W., Dummer, P.M., Etterson, M.A., Thogmartin, W.E., Wu, Q., Kannan, K., Trowbridge, A., McKann, P.C., 2014. Exposure and effects of perfluoroalkyl substances in tree swallows nesting in Minnesota and Wisconsin, USA. Arch. Environ. Contam. Toxicol. 66, 120–138. https://doi.org/10.1007/s00244-013-9934-0.

Custer, C.M., Custer, T.W., Delaney, R., Dummer, P.M., Schultz, S., Karouna-Renier, N., 2019. Perfluoroalkyl contaminant exposure and effects in tree swallows nesting at Clarks Marsh, Oscoda, Michigan, USA. Arch. Environ. Contam. Toxicol. 77, 1–13. https://doi.org/10.1007/s00244-019-00620-1.

Darras, V.M., 2022. Thyroid gland. In: Sturkie's Avian Physiology. Academic Press, Department of Biology. KU Leuven, Leuven, Belgium, pp. 815–832. https://doi.org/10.1016/B978-0-12-819770-7.00021-9.

Deeming, D.C., 2009. The role of egg turning during incubation. Avian Biol. Res. 2, 67–71. https://doi.org/10.3184/175815509X431849.

Dennis, N.M., Karnjanapiboonwong, A., Subbiah, S., Rewerts, J.N., Field, J.A., McCarthy, C., Salice, C.J., Anderson, T.A., 2020. Chronic reproductive toxicity of Perfluorooctane sulfonic acid and a simple mixture of Perfluorooctane sulfonic acid and perfluorohexane sulfonic acid to Northern bobwhite quail (Colinus virginianus). Environ. Toxicol. Chem. 39, 1101–1111. https://doi.org/10.1002/etc.4703.

DuRant, S.E., 2011. The role of incubation temperature in determining avian phenotype: implications for avian ecology. life history evolution, and conservation.

DuRant, S.E., Carter, A.W., Denver, R.J., Hepp, G.R., Hopkins, W.A., 2014. Are thyroid hormones mediators of incubation temperature-induced phenotypes in birds? Biol. Lett. 10, 20130950. https://doi.org/10.1098/rsbl.2013.0950.

D'Alba, L., Spencer, K.A., Nager, R.G., Monaghan, P., 2011. State dependent effects of elevated hormone: nest site quality, corticosterone levels and reproductive performance in the common eider. Gen. Comp. Endocrinol. 172, 218–224. https://doi.org/10.1016/j.ygcen.2011.03.006.

Frøyland, S.H., 2022. Per- and Polyfluoroalkyl Substances (Pfass) Concentrations over the Laying Sequence in Eggs of the Common Eider (Somateria mollissima) from the Baltic Sea in Relation to Sex Steroid Hormones (Master Thesis). NTNU.

Groffen, T., Buytaert, J., Prinsen, E., Bervoets, L., Eens, M., 2024. Per- and Polyfluoroalkyl Substances (PFAS) accumulation, reproductive impairment, and associations with nestling body condition in great (Parus major)- and blue tits (Cyanistes caeruleus) living near a hotspot in Belgium. Toxics 12, 636. https://doi.org/10.3390/toxics12090636.

Hartig, F., Lohse, L., 2022. Dharma: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.

Hellman, J., 2017. Haahkanaaraan (Somateria mollissima) Pitkäaikaisen Paaston Fysiologiset Vaikutukset. University of Helsinki (MSc thesis).

Hope, S.F., Buenaventura, C.R., Husain, Z., DuRant, S.E., Kennamer, R.A., Hopkins, W.A., Thompson, C.K., 2019. Limited support for thyroid hormone or corticosterone related gene expression as a proximate mechanism of incubation temperature-dependent phenotypes in birds. Front. Physiol. 10. https://doi.org/10.3389/fphys.2019.00857.

Hope, S.F., DuRant, S.E., Angelier, F., Hallagan, J.J., Moore, I.T., Parenteau, C., Kennamer, R.A., Hopkins, W.A., 2020. Prolactin is related to incubation constancy and egg temperature following a disturbance in a precocial bird. Gen. Comp. Endocrinol. 295, 113489. https://doi.org/10.1016/j.ygcen.2020.113489.

Hsu, B.-Y., Pakanen, V.-M., Boner, W., Doligez, B., Eeva, T., Groothuis, T.G.G., Korpimäki, E., Laaksonen, T., Lelono, A., Monaghan, P., Sarraude, T., Thomson, R.L., Tolvanen, J., Tschirren, B., Vásquez, R.A., Ruuskanen, S., 2022. Maternally transferred thyroid hormones and life-history variation in birds. J. Anim. Ecol. 91, 1489–1506. https://doi.org/10.1111/1365-2656.13708.

Ilvonen, R.-L.H., 2025. Site-, habitat-, and Predation Risk-dependent Incubation Patterns in Common Eider (Somateria mollissima) and their Links to Breeding Success. Helsingin yliopisto.

Jaatinen, K., Öst, M., Hobson, K.A., 2016. State-dependent capital and income breeding: a novel approach to evaluating individual strategies with stable isotopes. Front. Zool. 13, 24. https://doi.org/10.1186/s12983-016-0157-x.

Kelsey, E.C., Bradley, R.W., Warzybok, P., Jahncke, J., Shaffer, S.A., 2016. Environmental temperatures, artificial nests, and incubation of Cassin's auklet. J. Wildl. Manag. 80, 292–299. https://doi.org/10.1002/jwmg.1012.

Kilpi, M., Lindström, K., 1997. Habitat-specific clutch size and cost of incubation in common eiders, Somateria mollissima. Oecologia 111, 297–301. https://doi.org/10.1007/s004420050238.

Krishnan, G., Devaraj, C., Silpa, M.V., Sejian, V., 2023. Thermoregulation in birds. In: Das, P.K., Sejian, Veerasamy, Mukherjee, J., Banerjee, D. (Eds.), Textbook of Veterinary Physiology. Springer Nature, Singapore, pp. 751–764. https://doi.org/10.1007/978-981-19-9410-4_29.

Laurila, M., Pilto, T., Hohtola, E., 2005. Testing the flexibility of fasting-induced hypometabolism in birds: effect of photoperiod and repeated food deprivations. J. Therm. Biol. 30, 131–138. https://doi.org/10.1016/j.jtherbio.2004.09.002.

Lenth, R.V., Piaskowski, J., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Hervé, M., Jung, M., Love, J., Miguez, F., Riebl, H., Singmann, H., 2025. Emmeans: Estimated Marginal Means, Aka Least-Squares Means.

Liebezeit, J.R., Smith, P.A., Lanctot, R.B., Schekkerman, H., Tulp, I., Kendall, S.J., Tracy, D.M., Rodrigues, R.J., Meltofte, H., Robinson, J.A., Gratto-Trevor, C., Mccaffery, B.J., Morse, J., Zack, S.W., 2007. Assessing the development of shorebird eggs using the flotation method: Species-Specific and generalized regression models. Condor 109, 32–47. https://doi.org/10.1093/condor/109.1.32.

Lohmann, R., Abass, K., Bonefeld-Jørgensen, E.C., Bossi, R., Dietz, R., Ferguson, S., Fernie, K.J., Grandjean, P., Herzke, D., Houde, M., Lemire, M., Letcher, R.J., Muir, D., De Silva, A.O., Ostertag, S.K., Rand, A.A., Søndergaard, J., Sonne, C., Sunderland, E.M., Vorkamp, K., Wilson, S., Weihe, P., 2024. Cross-cutting studies of per- and polyfluorinated alkyl substances (PFAS) in Arctic wildlife and humans. Sci. Total Environ. 954, 176274. https://doi.org/10.1016/j.scitotenv.2024.176274.

Lunde, E., 2023. Per- and Polyfluoroalkyl Substances (Pfass) Exposure in the Common Goldeneye (Bucephala Clangula) and Potential Relation with Thyroid Hormones and Avian Influenza Rate (Master Thesis). NTNU.

Mattsson, A., Sjöberg, S., Kärrman, A., Brunström, B., 2019. Developmental exposure to a mixture of perfluoroalkyl acids (PFAAs) affects the thyroid hormone system and the bursa of Fabricius in the chicken. Sci. Rep. 9, 19808. https://doi.org/10.1038/s41598-019-56200-9.

McKechnie, A.E., Lovegrove, B.G., 2002. Avian facultative hypothermic responses: a review. Condor 104, 705–724. https://doi.org/10.1093/condor/104.4.705.

McNabb, F.M.A., 2007. The hypothalamic-pituitary-thyroid (HPT) axis in birds and its role in bird development and reproduction. Crit. Rev. Toxicol. 37, 163–193. https://doi.org/10.1080/10408440601123552.

Milonoff, M., Pöysä, H., Runko, P., 2002. Reproductive performance of Common Goldeneye Bucephala clangula females in relation to age and lifespan. Ibis 144, 585–592. https://doi.org/10.1046/j.1474-919X.2002.00098.x.

Milonoff, M., Pöysä, H., Runko, P., Ruusila, V., 2004. Brood rearing costs affect future reproduction in the precocial common goldeneye Bucephala clangula. J. Avian Biol. 35, 344–351. https://doi.org/10.1111/j.0908-8857.2004.03215.x.

Newsted, J.L., Coady, K.K., Beach, S.A., Butenhoff, J.L., Gallagher, S., Giesy, J.P., 2007. Effects of perfluorooctane sulfonate on mallard and northern bobwhite quail exposed chronically via the diet. Environ. Toxicol. Pharmacol. 23, 1–9. https://doi.org/10.1016/j.etap.2006.04.008.

Nordén, M., Berger, U., Engwall, M., 2016. Developmental toxicity of PFOS and PFOA in great cormorant (Phalacrocorax carbo sinensis), herring gull (Larus argentatus) and chicken (Gallus gallus domesticus). Environ. Sci. Pollut. Res. 23, 10855–10862. https://doi.org/10.1007/s11356-016-6285-1.

Öst, M., Steele, B.B., 2010. Age-specific nest-site preference and success in eiders. Oecologia 162, 59–69. https://doi.org/10.1007/s00442-009-1444-4.

Öst, M., Ydenberg, R., Kilpi, M., Lindström, K., 2003. Condition and coalition formation by brood-rearing common eider females. Behav. Ecol. 14, 311–317. https://doi.org/10.1093/beheco/14.3.311.

Öst, M., Lehikoinen, A., Jaatinen, K., 2022. Top–down effects override climate forcing on reproductive success in a declining sea duck. Oikos 2022, e08762. https://doi.org/10.1111/oik.08762.

Pöysä, H., Runko, P., Ruusila, V., Milonoff, M., 2001. Identification of parasitized nests by using egg morphology in the Common Goldeneye: an alternative to blood sampling. J. Avian Biol. 32, 79–82. https://doi.org/10.1034/j.1600-048X.2001.320112.x.

Pöysä, H., Arzel, C., Runko, P., Vakili, F.S., 2025. Costs of personality: bold incubating goldeneye females risk their lives when a predator attacks. Behav. Ecol. Sociobiol. 79, 83. https://doi.org/10.1007/s00265-025-03628-x.

R Core Team, 2024. R: a Language and Environment for Statistical Computing.

Ricolfi, L., Taylor, M.D., Yang, Y., Lagisz, M., Nakagawa, S., 2024. Maternal transfer of per- and polyfluoroalkyl substances (PFAS) in wild birds: a systematic review and meta-analysis. Chemosphere 361, 142346. https://doi.org/10.1016/j.chemosphere.2024.142346.

Robuck, A.R., Cantwell, M.G., McCord, J., Addison, L.M., Pfohl, M., Strynar, M.J., McKinney, R., Katz, D.R., Wiley, D.N., Lohmann, R., 2020. Legacy and novel Per- and Polyfluoroalkyl Substances (PFAS) in juvenile seabirds from the US Atlantic Coast. Environ. Sci. Technol. 54, 12938–12948. https://doi.org/10.1021/acs.est.0c01951.

Ruuskanen, S., Darras, V.M., de Vries, B., Visser, M.E., Groothuis, T.G.G., 2016. Experimental manipulation of food availability leads to short-term intra-clutch adjustment in egg mass but not in yolk androgen or thyroid hormones. J. Avian Biol. 47, 36–46. https://doi.org/10.1111/jav.00728.

Ruuskanen, S., Hsu, B.-Y., Heinonen, A., Vainio, M., Darras, V.M., Sarraude, T., Rokka, A., 2018. A new method for measuring thyroid hormones using nano-LC-MS/

MS. J. Chromatogr. B 1093–1094, 24–30. https://doi.org/10.1016/j.jchromb.2018.06.052.
Sebastiano, M., Jouanneau, W., Blévin, P., Angelier, F., Parenteau, C., Gernigon, J., Lemesle, J.C., Robin, F., Pardon, P., Budzinski, H., Labadie, P., Chastel, O., 2021. High levels of fluoroalkyl substances and potential disruption of thyroid hormones in three gull species from South Western France. Sci. Total Environ. 765, 144611. https://doi.org/10.1016/j.scitotenv.2020.144611.
Sebastiano, M., Jouanneau, W., Blévin, P., Angelier, F., Parenteau, C., Pallud, M., Ribout, C., Gernigon, J., Lemesle, J.C., Robin, F., Pardon, P., Budzinski, H., Labadie, P., Chastel, O., 2023. Physiological effects of PFAS exposure in seabird chicks: a multi-species study of thyroid hormone triiodothyronine, body condition and telomere length in South Western France. Sci. Total Environ. 901, 165920. https://doi.org/10.1016/j.scitotenv.2023.165920.
Shaffer, S.A., Clatterbuck, C.A., Kelsey, E.C., Naiman, A.D., Young, L.C., VanderWerf, E. A., Warzybok, P., Bradley, R., Jahncke, J., Bower, G.C., 2014. As the egg turns: monitoring egg attendance behavior in wild birds using novel data logging technology. PLoS One 9, e97898. https://doi.org/10.1371/journal.pone.0097898.
Shaffer, S.A., Blévin, P., Barbraud, C., Chastel, O., Weimerskirch, H., 2021. Comparative egg attendance patterns of incubating polar petrels. Anim. Biotelem. 9, 17. https://doi.org/10.1186/s40317-021-00240-4.
Sonne, C., Siebert, U., Gonnsen, K., Desforges, J.-P., Eulaers, I., Persson, S., Roos, A., Bäcklin, B.-M., Kauhala, K., Tange Olsen, M., Harding, K.C., Treu, G., Galatius, A., Andersen-Ranberg, E., Gross, S., Lakemeyer, J., Lehnert, K., Lam, S.S., Peng, W., Dietz, R., 2020. Health effects from contaminant exposure in Baltic Sea birds and marine mammals: a review. Environ. Int. 139, 105725. https://doi.org/10.1016/j.envint.2020.105725.
Spulber, S., Kilian, P., Ibrahim, W.N.W., Onishchenko, N., Ulhaq, M., Norrgren, L., Negri, S., Tuccio, M.D., Ceccatelli, S., 2014. PFOS induces behavioral alterations, including spontaneous hyperactivity that is corrected by dexamfetamine in zebrafish Larvae. PLoS One 9, e94227. https://doi.org/10.1371/journal.pone.0094227.
Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol. Evol. 8, 1639–1644. https://doi.org/10.1111/2041-210X.12797.
Sun, J., Letcher, R.J., Waugh, C.A., Jaspers, V.L.B., Covaci, A., Fernie, K.J., 2021. Influence of perfluoroalkyl acids and other parameters on circulating thyroid hormones and immune-related microRNA expression in free-ranging nestling peregrine falcons. Sci. Total Environ. 770, 145346. https://doi.org/10.1016/j.scitotenv.2021.145346.
Sun, J., Xing, L., Chu, J., 2023. Global ocean contamination of per- and polyfluoroalkyl substances: a review of seabird exposure. Chemosphere 330, 138721. https://doi.org/10.1016/j.chemosphere.2023.138721.
Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65, 13–21. https://doi.org/10.1007/s00265-010-1037-6.
Taylor, G.T., Ackerman, J.T., Shaffer, S.A., 2018. Egg turning behavior and incubation temperature in Forster's terns in relation to mercury contamination. PLoS One 13, e0191390. https://doi.org/10.1371/journal.pone.0191390.
The MathWorks, Inc., 2020. MATLAB (R2020a). Natick, MA, USA.
Thierry, A.-M., Brajon, S., Massemin, S., Handrich, Y., Chastel, O., Raclot, T., 2013a. Decreased prolactin levels reduce parental commitment, egg temperatures, and breeding success of incubating male Adélie penguins. Horm. Behav. 64, 737–747. https://doi.org/10.1016/j.yhbeh.2013.06.003.
Thierry, A.-M., Massemin, S., Handrich, Y., Raclot, T., 2013b. Elevated corticosterone levels and severe weather conditions decrease parental investment of incubating Adélie penguins. Horm. Behav. 63, 475–483. https://doi.org/10.1016/j.yhbeh.2012.12.011.
Trimmel, S., Vike-Jonas, K., Gonzalez, S.V., Ciesielski, T.M., Lindstrøm, U., Jenssen, B.M., Asimakopoulos, A.G., 2021. Rapid determination of Per- and Polyfluoroalkyl Substances (PFAS) in Harbour porpoise liver tissue by HybridSPE®–UPLC®–MS/MS. Toxics 9, 183. https://doi.org/10.3390/toxics9080183.
Vainio, R.K., 2022. Apex avian species as sentinels for legacy and emerging contaminants in northern Baltic Sea coastal food webs. fi=Turun yliopisto|en=University of Turku|.
Vakili, F.S., Pöysä, H., Liehrmann, O., Runko, P., Björkman, S., Arzel, C., 2025. The older the bolder: common goldeneye antipredator behaviour based on long-term individual data. Anim. Behav. 220, 123046. https://doi.org/10.1016/j.anbehav.2024.12.002.
Verboven, N., Tinbergen, J.M., 2002. Nest desertion: a trade-off between current and future reproduction. Anim. Behav. 63, 951–958.
Waldeck, P., Kilpi, M., Öst, M., Andersson, M., 2004. Brood parasitism in a population of common eider (somateria Mollissima). Behaviour 141, 725–739. https://doi.org/10.1163/1568539042245132.
Westfall, P.H., Young, S.S., 1993. Resampling-Based Multiple Testing: Examples and Methods for p-Value Adjustment. John Wiley & Sons.
Xiao, F., 2017. Emerging poly- and perfluoroalkyl substances in the aquatic environment: a review of current literature. Water Res. 124, 482–495. https://doi.org/10.1016/j.watres.2017.07.024.
Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.