Science of the Total Environment 807 (2022) 150882

Contents lists available at ScienceDirect

Science of the Total Environment

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

Exposure to cumulative stressors affects the laying phenology and incubation behaviour of an Arctic-breeding marine bird

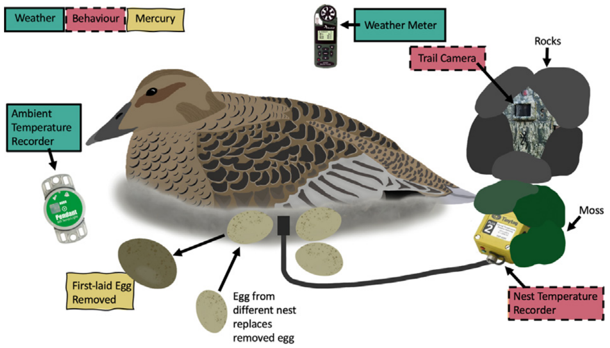
Reyd A. Smith [a,*], Saya S. Albonaimi [a], Holly L. Hennin [b], H. Grant Gilchrist [b], Jérôme Fort [c], Kyle J.L. Parkinson [a], Jennifer F. Provencher [d], Oliver P. Love [a]

[a] *University of Windsor, Windsor, Ontario N9B 3P4, Canada*
[b] *Wildlife Research Division, Environment and Climate Change Canada, Ottawa, Ontario K0A 1H0, Canada*
[c] *Littoral, Environnement et Sociétés (LIENSs), UMR 7266 CNRS – La Rochelle Université, 17000 La Rochelle, France*
[d] *Ecotoxicology and Wildlife Health Division, Environment and Climate Change Canada, Ottawa, Ontario K0A 1H0, Canada*

HIGHLIGHTS

- Effects of multiple stressors on egg laying behaviour for eiders were investigated.
- Higher air temperatures and higher [Hg] interactively related to earlier lay dates.
- Greater incubation disturbances occurred along with lower wind speeds.
- Higher temperatures and lower [Hg] interactively lead to greater disturbances.
- Multiple stressors may have cumulative costs that spread across breeding stages.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 11 August 2021
Received in revised form 4 October 2021
Accepted 4 October 2021
Available online 8 October 2021

Editor: Mae Sexauer Gustin

Keywords:
Multiple stressors
Mercury
Climate change
Common eider
Physiology

ABSTRACT

Wildlife are exposed to multiple stressors across life-history stages, the effects of which can be amplified as human activity surges globally. In Arctic regions, increasing air and ocean temperatures, more severe weather systems, and exposure to environmental contaminants all represent stressors occurring simultaneously. While Arctic vertebrates, including marine birds, are expected to be at risk of adverse effects from these individual stressors, few studies have researched their combined impacts on breeding behaviour and reproductive success. The interactive effects of environmental conditions and mercury (Hg) contamination on laying phenology and incubation behaviour were examined in female common eiders (*Somateria mollissima*, mitiq, ᒥᑎᖅ ᐊᒪᐅᓕᒡᔪᐊᖅ) nesting at Canada's largest Arctic breeding colony. Conditions with higher pre-breeding air temperatures were linked to females with higher egg Hg concentrations laying earlier than those with lower Hg values. Furthermore, examination of a total of 190 days of incubation behaviour from 61 eiders across two years revealed a negative relationship between wind speed and the frequency of incubation interruptions. Importantly, exposure to higher air temperatures combined with lower Hg concentrations was significantly correlated with increased incubation interruptions. Although previous research has shown that warmer spring temperatures could afford lower quality females more time to improve body condition to successfully lay, results suggest these females may face stronger cumulative fitness costs during incubation in warmer years, potentially in combination with the effects of Hg on physiological stress and hormone secretion. This study highlights how multiple stressors exposure, driven by human-induced environmental changes, can have a complex influence on reproduction.

---

* Corresponding author.
E-mail address: smith1ax@uwindsor.ca (R.A. Smith).

https://doi.org/10.1016/j.scitotenv.2021.150882
0048-9697/

1. Introduction

Climate change is changing environmental conditions in Arctic regions through expansive reductions in sea ice cover, increased frequency, severity, and unpredictability of extreme climatic events, and elevated air temperatures now three times the global average (Zhang, 2005; Hoegh-Guldberg and Bruno, 2010; Timmermans et al., 2011; AMAP, 2021). These climatic alterations have the potential to affect Arctic species, with effects ranging from changes in primary productivity abundance and phenology, to alterations in prey availability for top marine and terrestrial predators in a complex, connected system (Frederiksen et al., 2006; Renaut et al., 2018; Pratte et al., 2019; Lewis et al., 2020). Marine birds, in particular, are known to be highly sensitive to environmental change and elevated thermal environments (Piatt et al., 2007; Le Bohec et al., 2013; Choy et al., 2021). Environmental shifts can alter avian migratory and reproductive phenology, especially in the Arctic which offers a short favorable window for those breeding, notably via spatio-temporal constraints in prey availability at extreme latitudes (Martin and Wiebe, 2004). Higher air temperatures have been shown to directly impact reproduction by advancing lay dates, accelerating embryonic growth, and decreasing incubation attentiveness in birds (Camfield and Martin, 2009; Visser et al., 2009; Durant et al., 2010; Nord and Nilsson, 2011). Lowered incubation attentiveness can not only extend the incubation period and potentially impact successful hatching and fledging through heightened predation risk (Conway and Martin, 2000; Smith et al., 2012; Higgott et al., 2020), but it can also leave the female in worse body condition relative to females with lower incubation effort through increased time spent maintaining optimal clutch temperature (Bottitta et al., 2003; D'Alba et al., 2009; Høyvik Hilde et al., 2016). In relation to thermal conditions, higher wind speeds can result in increased incubation effort and higher body mass loss (Kilpi and Lindström, 1997; Høyvik Hilde et al., 2016). In contrast, low wind speeds when combined with high temperatures can instead exacerbate incubation effort due to birds exceeding their thermal neutral zones (Fast et al., 2007), with downstream negative effects on embryonic development time, egg and duckling predation risk, therefore risking costs to female's fitness (Hanssen et al., 2005; Martin et al., 2015).

While the impacts of climate change on Arctic species are well appreciated (Møller et al., 2010; Wassmann et al., 2011; Descamps et al., 2017), these ecosystems now face many additional and simultaneous environmental stressors. Many contaminants exist in the Arctic in relatively high concentrations from long-range transport towards the poles by air and ocean currents, as well as via the melting of permafrost and glaciers that release contaminants stored from decades of elevated contaminant output (Macdonald et al., 2000; Kirk et al., 2012; Schuster et al., 2018; Hawkings et al., 2021). Mercury (Hg) has been noted as a research priority in Arctic marine systems because of its higher rates of contamination relative to terrestrial systems and its toxic effects across multiple vertebrate taxa (Provencher et al., 2014; Adlard et al., 2018; Gundersen et al., 2020). In marine birds, Hg contamination even at low concentrations can have system wide, adverse effects on neurology, physiology, behaviour, and reproduction (Albers et al., 2007; Ackerman et al., 2016a; Whitney and Cristol, 2017; Pollet et al., 2017). Sub-lethal Hg has been correlated with a decrease in the likelihood to breed in marine birds, mechanistically linked with reductions in key reproductive hormones (e.g., luteinizing hormone, estrogens), as well as the growth of gonadal tissues (Tartu et al., 2013, 2014). The effects of Hg exposure can also affect later stages of breeding through reductions in incubation consistency, measured as the frequency of incubation interruptions (Bustnes et al., 2001). These effects are likely mediated by the endocrine-disrupting effect of Hg on prolactin (PRL), a hormone key in forming and maintaining parental attachment to the nest (El Halawani et al., 1984; Tartu et al., 2015, 2016; Angelier et al., 2016). Overall, exposure to multiple environmental stressors can have downstream effects on reproductive success and survival (Bustnes et al., 2001; Visser et al., 2009; Durant et al., 2010; Nord and Nilsson, 2011; Hallinger and Cristol, 2011). As such, accounting for multiple stressors in an interactive effect framework is now considered vital for determining how individually mediated processes will impact population and ecosystem processes (Vinebrooke et al., 2004; Schindler and Smol, 2006). However, while the combined effects of these stressors are expected to be a 'worst-case scenario' for Arctic species (Jenssen, 2006; Borgå, 2019), few studies outside of temperate systems have been able to examine the cumulative effects of multiple stressors on key mechanisms driving reproductive performance and fitness (Crain et al., 2008; Andersen et al., 2017; Bårdsen et al., 2018; Amélineau et al., 2019).

The interactive effects of environmental conditions and maternal Hg concentrations (using first-laid eggs as a proxy) in relation to lay date phenology and incubation behaviour were examined in a long-lived Arctic-breeding marine bird, common eider (*Somateria mollissima*, hereafter eiders), or mitiq (ᒥᑎᖅ ᐊᒪᐅᓕᒡᔪᐊᖅ) in Inuktitut. Eiders use a capital-income based reproductive strategy by utilizing a combination of stored fat from the wintering grounds and incoming resources from intensive pre-breeding foraging during migration and at the breeding site to support reproduction (Sénéchal et al., 2011). Females that can obtain the needed endogenous stores more quickly are able to lay earlier, invest in larger clutch sizes, and increase offspring recruitment (Love et al., 2010; Descamps et al., 2011; Hennin et al., 2018). In the first objective, lay date was related independently and interactively to individual air temperature, wind speed exposure as well as egg Hg concentrations (a direct proxy for female Hg burden at the time of laying; Evers et al., 2003; Brasso et al., 2010; Ackerman et al., 2016b). It was hypothesized that lay date would vary between sampling years potentially due to annual environmental and phenological differences in prey availability. An additional hypothesis was that individuals with higher egg Hg concentrations, exposure to higher air temperatures and higher wind speeds would result in later lay dates.

After the pre-breeding foraging period when appropriate body condition has been met for breeding, female eiders undergo a uni-parental 24–26 day incubation fast in which they mobilize their endogenous fat and protein reserves (Hanssen et al., 2002; Bottitta et al., 2003; Sénéchal et al., 2011). During their incubation fast and as incubation advances from early to late stages, eiders release and circulate contaminants accumulated within their tissues that may influence incubation behaviour (Wayland et al., 2005; Bustnes et al., 2010; McPartland et al., 2020). The effects of Hg could be further amplified by extreme air temperature and wind speed exposure during the incubation period by affecting metabolic rates of the incubating female (e.g., Fast et al., 2007) and influencing rates of body mass loss and immune system functioning (Bourgeon and Raclot, 2006, 2007). As such, in our second objective, the influence of air temperature, wind speeds, and egg Hg concentrations on variation in incubation interruptions was examined. It was hypothesized that higher egg Hg concentrations, high air temperature and lower wind speeds would result in higher incubation disruptions. Overall, by examining the impact of multiple environmental stressors on incubation phenology and behaviour, we aimed to identify whether multiple stressors influence eider incubation and the potential contributors influencing incubation success in a rapidly changing ecosystem.

2. Methods

2.1. Study site and data collection

The focal study system was female common eiders nesting at the East Bay Island colony (Mitivik Island, Nunavut, Canada; 64°02′N, 81°47′W), located within in the Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary. The study period ranged from late June to mid-July in 2016 ($n = 13$), 2017 ($n = 12$), 2018 ($n = 46$) and 2019 ($n = 38$, total $N = 109$), commencing when females throughout the colony began incubation. Active nests were located using spotting scopes from six observation blinds distributed across the colony from 2016 to 2019, with additional nests located opportunistically in 2018–2019. To quantify nest environmental conditions and incubation behaviour, in 2018 and 2019 between 1 and 13 days after a female laid her first egg, temperature-recording pendants (HOBO Pendant® MX2201 and 64 K) were deployed ~0.5 m away from each incubating hen at nest level to quantify ambient air temperature every minute. A Kestrel 5500 weather meter was placed approximately 3-m off the ground in five dispersed locations across the colony to collect data on average wind speed each hour. Behaviour monitoring equipment was placed at each nest, consisting of a nest temperature probe (Tinytag® Plus 2) and a trail camera (Browning 2018 Strike Force Pro). Temperature probes were placed at the bottom of the nest in the middle of the clutch of eggs to record nest temperature every minute for the duration of that individual nest's incubation period, providing a proxy of incubation interruptions given that while hens are sitting on eggs, the nest temperature is higher than external air temperature. Motion-activated trail cameras were placed ~1 m away from the nest cup to corroborate incubation interruption data from the temperature probes and, when possible, determine the cause of nest failure (predation, abandonment). All behaviour and environmental monitoring equipment were left in place to collect data for the duration of incubation (roughly 3 weeks), after which all the equipment was retrieved. From the original 84 nests with monitoring equipment deployed (in 2018–2019), 61 nests (73%, $n = 31$; 2018, $n = 30$; 2019) had useable data for analysis, while the remaining 23 nests were unusable due to nest predation by polar bears (*Ursus maritimus*) and/or gulls (*Larus* species), hen nest abandonment, or removal of the nest temperature probe by the incubating female (0–3 days post deployment; see Statistical analyses).

2.2. Egg mercury analysis

In 2016–2017, whole clutches of eggs were collected from nests, with only the first-laid egg being used for this study. However, in 2018–2019 when incubation behaviour was measured, only the female's first-laid egg was collected for Hg analysis (as determined by the observable larger size and darker colouration; Erikstad et al., 1998). Egg collection was done during the deployment of the incubation monitoring equipment, during which the removed egg was replaced with a common eider egg from a nearby nest to maintain clutch size consistency and incubation energetics for the behaviour analysis in these years. For each year of collection, every collected egg was measured and candled to obtain approximate egg age, and therefore estimate lay date and incubation initiation for each nest (Reiter and Andersen, 2008; Garbus et al., 2018). Eggs were frozen at −20 °C within 24 h of collection until further analysis.

First-laid common eider eggs that were collected from 2016 to 2019 (see Study site and data collection) were individually thawed and the shells were removed for sub-sampling. A total of 1.5 mL of both albumen and yolk samples were placed into individual cryovials, and then re-froze samples at −20 °C. Cryovials for sample storage were acid-washed for two days using 65% nitric acid (CAS# 7697-37-2) diluted to 20% concentration with Ultrapure water, then rinsed three times with Ultrapure water. All materials used to dissect eggs were rinsed with Ultrapure water, followed by acid-washing for 10 min to minimize cross-contamination, then another rinse with Ultrapure water before dissection. Samples were freeze-dried for approximately 72 h, after which they were ground into a fine, homogenized powder using a metal spatula cleaned with acetone.

Analysis of egg Hg concentrations was conducted at the Littoral Environment et Sociétés institute (LIENSs, La Rochelle, France) using the yolk and albumen from each first-laid eider egg collected across all four sampling years ($n = 121$). Total Hg (THg) concentrations were determined in this study as it has been shown in avian eggs to primarily consist of MeHg (methylmercury), the most highly toxic and biologically mobile form of Hg (Ackerman et al., 2013). Freeze-dried yolk and albumen samples were analyzed using an Advanced Hg Analyzer spectrophotometer (Altec AMA 254) set at a detection limit of 0.10 ng dry weight (dw). The quality control program included running blanks prior to the analysis, as well as analyzing reference materials from lobster hepatopancreas (TORT-3) from the National Research Council (NRC), Canada (reference values were 0.292 ± 0.022 μg/g dw SD, mean measured ± SD = 0.285 μg/g dw, recovery = 1.69%) every 15 samples. Whole egg THg concentrations were calculated for each egg from the yolk and albumen values using a known eider yolk:albumen ratio of 1:1 (yolk $*$ 0.5 + albumen $*$ 0.5; Swennen and Van der Meer, 1995). All THg concentrations are reported in μg/g dw.

2.3. Statistical analyses

2.3.1. Variation in lay date phenology

Eiders form their eggs during a period of rapid follicle growth (RFG; the initiation of yolk formation that occurs seven days before laying of the first egg in eiders; Hennin et al., 2015). Therefore, the initiation of the RFG was calculated using each hen's lay date (lay date − 7 days). Data on average air temperature and wind speed over the seven days prior to the RFG initiation period for each female was collected from the weather station at Coral Harbour (64°11′N, 83°21′W; 68 km from East Bay) using Environment and Climate Change Canada (ECCC)'s online database (https://climate.weather.gc.ca/index_e.html). These local temperature and wind values were then used in the model to represent the pre-breeding environmental conditions (Love et al., 2010).

Data from 2016 to 2019 inclusive was used to examine how air temperature, wind speed and THg concentrations combined to influence individual lay date. Specifically, a Generalized Linear Model (GLM) was conducted using R version 3.6.2 (R Development Core Team) with ordinal lay date as the dependent variable. Local air temperature and wind speed during the RFG period as well first-laid egg THg concentrations were included as independent variables individually and in all possible 2-way interactions, as well as a 3-way interaction. Sampling year was also included as an independent continuous variable, since having it as a categorical variable caused model overfitting. All variables in the interactions were standardized and centered for comparison and to reduce the misrepresentation of effects and improve the interpretability of coefficients (Schielzeth, 2010). Year was also included as a fixed variable but excluded from interactions. All assumptions for a GLM were met by visually inspecting histograms to confirm a normal distribution of the data, quantile-quantile plots, and residual plots from model outputs, as well as confirming no multicollinearity between all variables, most notably wind speed and air temperature ($r = -0.09$, variance inflation factor (VIF) = 1.05).

2.3.2. Variation in incubation behaviour (nesting disturbances)

Incubation behaviour was examined in 2018–2019 by quantifying the number of incubation interruptions as determined by an abrupt shift in nest temperature, preceded and followed by a period of stationary nest temperature. Two separate viewers initially corroborated the nest temperature data using video footage from the trail cameras to independently train the viewers on how to accurately interpret female nest movements using the nest temperature data. This was followed by the determination of incubation interruptions using nest temperature data without consulting the video footage to make up the final, complete dataset. Recesses away from the nest were counted as one incubation interruption and validated with associated trail camera footage when available. Incubation interruptions were determined over two consecutive 24-hour periods in each third of incubation during early (days 4–7; $n = 49$), middle (days 12–15; $n = 36$), and late stages (days 18–24; $n = 10$, see Supplemental materials) whenever available before incubation termination for each of the 61 nests (Bourgeon et al., 2006). These specific ranges in incubation day were chosen to obtain the highest sample size for each incubation stage while maintaining a spread of at least five days between stages for each hen. To account for differences in behaviour across the day, each 24-hour period was separated into four, 6-hour sections (0:00–5:59; Section 1, 6:00–11:59; Section 2, 12:00–17:59; Section 3, 18:00–23:59; Section 4; see Supplemental materials), and the number of incubation interruptions was determined for each female within each of these periods for subsequent analysis.

Next, the effects of female-specific environmental exposure to wind speeds individually, as well as air temperature individually and in combination with THg concentrations, were examined in relation to her incubation interruptions. A Generalized Linear Mixed Model (GLMM) was conducted to examine whether exposure to multiple stressors influenced incubation interruptions using the square-root transformed number of incubation interruptions in each section of the day as the dependent variable. Average air temperature and wind speed for each of the four sections of the day, as well as individual whole egg THg concentrations were included as independent variables. Additionally, the interaction between air temperature and THg concentrations was included, with both variables centered and standardized (Schielzeth, 2010). Interactions involving wind speed were excluded from the final model since they were not significant and prevented model convergence. Section of the day (1–4), incubation stage (early, mid, late), and individual ID (0–61) were included as categorical random variables. Year was removed from this analysis because it explained close to 0% of the variance in the dependent variable. Further examinations into whether individual incubation interruptions varied in response to the stage of incubation and section of the day as defined above revealed no significant correlations, however, they remained important covariates in the model.

The effect sizes of the statistically significant individual variables were calculated and compared to established standards of low (0.2), medium (0.6), and large (0.8; see Cohen, 1988). The effect sizes of statistically significant interactions were also calculated and compared to established values of low (0.4), medium (1.0), and large effects (1.6; Bodner, 2017) to further disentangle their impacts on incubation interruptions. All assumptions were met for the GLMM by visually inspecting histograms to confirm normal distribution of the data, quantile-quantile plots, and residual plots from model outputs, determining no overdispersion, as well as determining a lack of multicollinearity between temperature and wind variables ($r = -0.07$, $VIF = 1.01$). Further, as the correlation coefficient for each interaction does not inform us of the positive or negative direction for all variables within the interaction, significant interactive model outputs were separately graphed using the R package Interactions v.1.1.3 (Long, 2019).

3. Results

3.1. Relationship between multiple environmental stressor exposure and lay date

First-laid eggs from 2016 to 2019 had an average THg level of 0.07 ± 0.03 μg/g dry weight (dw) in yolk (range 0.022–0.191 μg/g dw), and 2.17 ± 0.87 μg/g dw in albumen (range 0.60–5.36 μg/g dw) for all years combined (Table 1). Calculation of egg homogenate from the yolk and albumen results gave an average of 1.12 ± 0.44 μg/g dw (range 0.31–2.72 μg/g dw; Table 1).

Lay date had a positive correlation with sampling year, with a range of 10 days in average lay date between 2016 and 2019 (Table 2A; Supplemental materials). Additionally, the parameter associated with the interaction between air temperature and wind speed was significant. As both temperature and wind speeds increased, birds had later lay dates (Table 2A; Fig. 1). Furthermore, the interaction between air temperature and THg concentrations had a significant relationship with lay date (Table 2A; Fig. 1). Specifically, higher air temperatures and lower THg concentrations correlated with the latest lay dates (Fig. 1). The effect size for air temperature alone was 1.02, considered a strong effect (Cohen, 1988), while the interaction between temperature and THg was calculated to be 1.11, considered to be a medium interactive effect (Bodner, 2017).

Table 1
Total Hg content (in μg/g dry weight) of 121 first-laid common eider eggs at East Bay Island (Mitivik), Nunavut, Canada across four consecutive years including 2016 ($n = 13$), 2017 ($n = 12$), 2018 ($n = 46$) and 2019 ($n = 50$). Table includes the yolk, albumen, and total egg values (yolk ∗ 0.5 + albumen ∗ 0.5; Swennen and Van der Meer, 1995).

	Mean	Standard deviation	Range
2016			
Yolk	0.06	0.02	0.04–0.11
Albumen	2.49	0.86	1.23–4.11
Total egg	1.28	0.44	0.68–2.11
2017			
Yolk	0.08	0.02	0.05–0.12
Albumen	2.86	1.21	1.24–5.37
Total egg	1.47	0.61	0.65–2.72
2018			
Yolk	0.07	0.02	0.02–0.14
Albumen	2.08	0.80	0.88–4.29
Total egg	1.08	0.41	0.47–2.19
2019			
Yolk	0.07	0.03	0.02–0.19
Albumen	2.00	0.75	0.60–0.41
Total egg	1.03	0.38	0.31–2.12
All years			
Yolk	0.07	0.03	0.02–0.19
Albumen	2.17	0.87	0.60–5.36
Total egg	1.12	0.44	0.31–2.72

3.2. Effects of exposure to multiple stressors on incubation interruption

Across all females in 2018 and 2019, incubation interruptions occurred 25 ± 6 times a day (years combined – see Statistical analyses section of the Methods), with the most attentive eider having 13 incubation interruptions in one day and the most restless female having 45 incubation interruptions. During early incubation, interruptions occurred 26 ± 6 times, mid-stage interruptions occurred 24 ± 6 times, and during late-stage incubation interruptions occurred 23 ± 6 times a day.

Results indicated that exposure to higher temperatures and low wind speeds was related to greater incubation disturbances (Table 2). Further, the interaction between higher temperature and lower egg THg concentrations was marginally significant ($p = 0.05$) and correlated with a greater number of incubation interruptions (Table 2C,

Table 2
Results of two statistical models examining a) predictors of lay date (objective a), and (b) the number of incubation interruptions by individual weather exposure of common eider at East Bay Island (Mitivik), Nunavut, Canada (objective b), with random effects including the number of incubation interruptions by incubation stage, hen ID (0–61), and section of the day (0:00–5:59, 6:00–11:59, 12:00–17:59, 18:00–23:59). Objective (a) used data collected from 2016 to 2019 ($n = 86$), while objective (b) used data only from 2018 and 2019 ($n = 61$). Significant *p*-values are bolded.

Variable	Estimate (β)	SE	t	p-Value
(a) Lay date – Generalized Linear Model				
Intercept	1935.231	782.138	2.474	**0.016**
Year	−0.873	0.388	−2.251	**0.027**
Temperature	4.039	0.441	9.152	**<0.001**
Wind	−0.335	0.341	−0.984	0.328
THg	−0.054	0.331	−0.162	0.872
Temp:Wind	2.059	0.370	5.562	**<0.001**
Temp:THg	−0.781	0.334	−2.337	**0.022**
Wind:THg	0.172	0.311	0.554	0.581
Temp:Wind:THg	−0.206	0.326	−0.632	0.529
(b) Incubation interruptions – Generalized Linear Mixed Model				
Intercept	2.499	0.067	37.521	<0.001
Temperature	0.111	0.029	3.814	**0.005**
Wind	−0.007	0.003	−2.783	**0.005**
THg	−0.003	0.032	0.010	0.991
Temp:THg	−0.025	0.013	−1.926	**0.054**

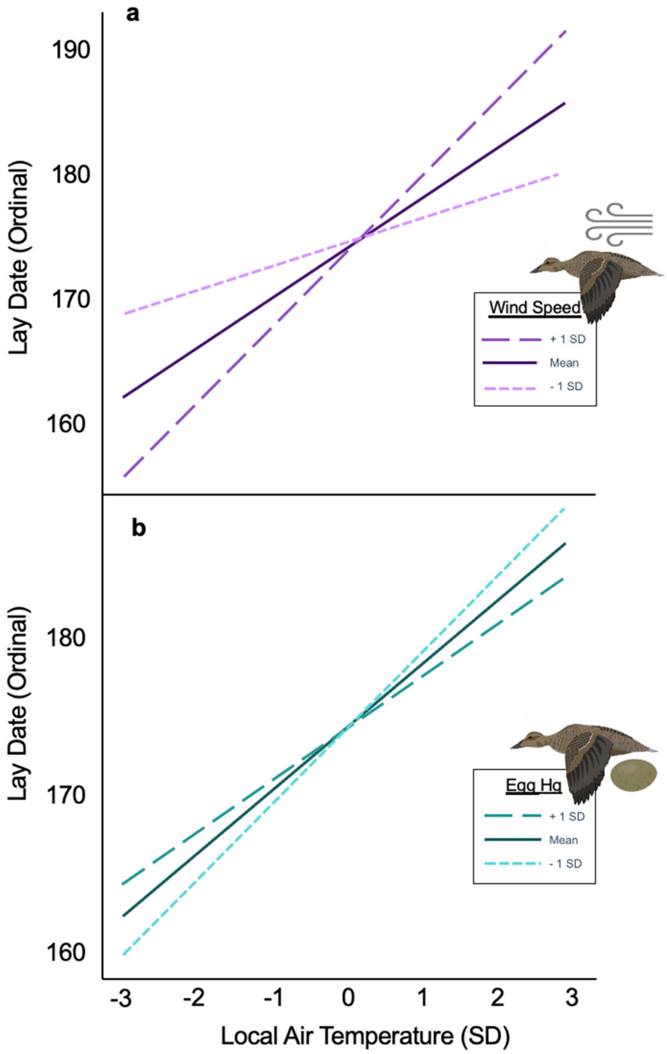


Fig. 1. Output from a GLM (Generalized Linear Model) with a normal distribution, showing significant patterns between a) air temperature (°C) standard deviation (SD) and wind speed (km/h) (both measured over the five days prior to the rapid follicle growth (RFG) period) and b) air temperature (°C) SD and egg THg concentrations (μg/g dry weight) in explaining variation in common eider lay date (ordinal) from 2016 to 2019 at East Bay Island (Mitivik), Nunavut, Canada.

Fig. 2). The effect size for temperature individually was 0.18, and therefore considered a small effect (Cohen, 1988). However, the effect size for the interaction between temperature and THg on incubation interruptions was 0.28, which although still considered a small effect, was larger than temperature alone (Bodner, 2017).

4. Discussion

The overall aim of this study was to examine the simultaneous effects of multiple stressors on common eider reproductive phenology and incubation interruptions by determining how these factors varied with air temperature, wind speed, and THg concentrations. In the pre-breeding period, local air temperature, wind speed and egg THg concentrations all influenced lay date. Temperature had the strongest singular effect and generated a significant interaction with both wind speed and THg concentrations to influence laying date. This suggests that birds with the latest lay dates were associated with exposure to higher air temperatures individually and in an interaction with higher wind speeds, as well as in an interaction with lower egg THg concentrations. Notably, egg THg concentrations were above levels seen previously at this site from eggs collected a decade before (2008: 0.50 μg/g dw, range 0.37–0.58; Akearok et al., 2010). Furthermore, nest-level air temperature and wind speed during incubation showed the strongest relationship with incubation behaviour itself, with THg having a marginally significant effect on incubation interruptions in an interaction with air temperature. These patterns suggest that exposure to lower winds, and higher air temperatures individually, and when combined with lower THg concentrations were correlated with greater incubation interruptions.

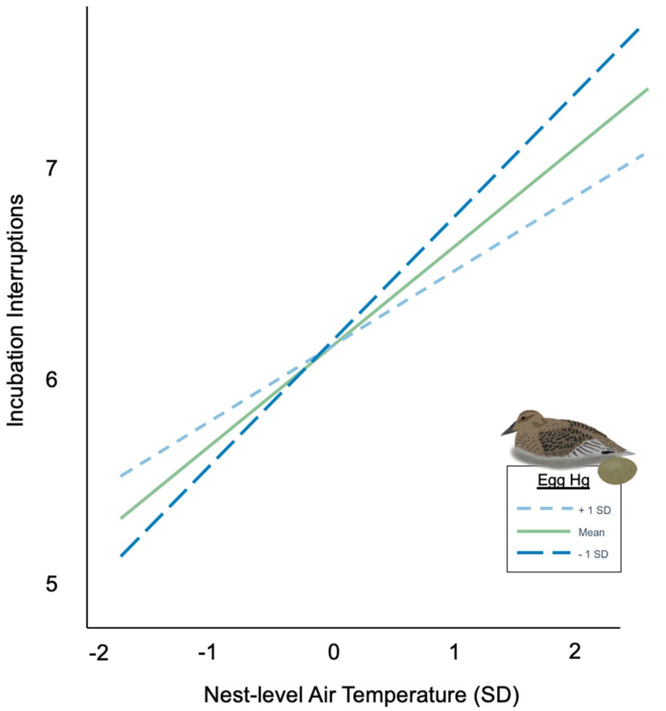


Fig. 2. Output from a GLMM (Generalized Linear Mixed Model) with a normal distribution, showing the interaction between nest-level air temperature (°C), and total first-laid egg Hg (μg/g dry weight) represented by standard deviations (SD) from the mean. Shown is the interaction explaining variation in the number of on-nest movements a female common eider made over a 6-hour period during incubation (data collected in July 2018 and 2019 from 61 eider nests located at East Bay Island (Mitivik), Nunavut, Canada).

4.1. Influence of multiple environmental stressor exposure on laying phenology

Lay date varied with sampling year and was the earliest in 2019, which is likely related to warmer spring temperatures and more available pre-breeding prey resources. These relationships have been demonstrated in previous research (Love et al., 2010; Jean-Gagnon et al., 2018), indicating that eider ducks may potentially benefit from a warmer year by easing environmental constraints on foraging through a reduction in land-fast sea ice in East Bay. Warmer springs may extend spatiotemporal access to available local prey, allowing lower quality (i.e., lower body condition) females the ability to improve body condition enough to lay (Love et al., 2010; Jean-Gagnon et al., 2018). Additionally, earlier laying females were exposed to both lower air temperatures and higher wind speeds during the RFG period in a significant 2-way interaction. This relationship suggests that the influence of wind speed on the timing of laying is an important factor as temperature effects may be exaggerated further when also considering wind speed.

Importantly, the advanced melting of snow and ice due to warmer spring temperatures may release more THg into the environment that, if coinciding with intensified eider pre-breeding foraging, could lead to increased THg exposure in eiders preparing to breed (Macdonald et al., 2000; Kirk et al., 2012; Schuster et al., 2018; Hawkings et al., 2021). Importantly, this link between egg Hg concentrations and spring freshet has recently been demonstrated in western Canada in gulls and terns (Hebert et al., 2021). We recognize that in this study system a time lag may exist between when inorganic Hg, released from melting ice, is converted into MeHg and is then accumulated in birds and may reflect in inter-annual variation in eider Hg concentrations (Foster et al., 2019). However, in this study lay date varied significantly with an interaction between air temperature and THg, where higher air temperatures, together with lower THg concentrations, were associated with later laying dates (Fig. 1). Although counterintuitive that higher THg concentrations were correlated with earlier laying, this trend may be explained by previous research examining links between THg, corticosterone (CORT, a glucocorticoid stress hormone), body condition, foraging intensity, and arrival date. In previous studies at East Bay Island, earlier arriving female eiders, which also lay earlier (Descamps et al., 2011), were found to have lower CORT concentrations (Hennin et al., 2015, 2018). Furthermore, research has shown that seabirds with elevated THg concentrations also had lower CORT and lowered body condition, likely influenced by the endocrine disrupting effects of THg (Fort et al., 2014; Provencher et al., 2016). These findings suggest that higher temperatures may lead to greater foraging opportunities due to earlier sea ice melt, ultimately allowing for more quickly improved body condition and less associated energetic stress. Thus, birds with greater THg concentrations may be at a disadvantage due to a further reduction in CORT that prevents more rapidly improved body condition through reduced foraging effort. Moreover, eiders at East Bay are known to shift prey selection along with laying phenology, with birds laying later utilizing bivalves as a prey source, compared to amphipods by those eiders laying earlier (Sénéchal et al., 2011). This prey shift apparently occurs as sea ice break-up makes benthic feeding areas increasingly accessible to diving eider ducks (Sénéchal et al., 2011). Since prey choice and primary production conditions are known to influence eider Hg concentrations, eiders that rely on lower trophic level bivalves rather than higher trophic level amphipods may accumulate less Hg (Mallory et al., 2010; Clayden et al., 2015; Smith et al., 2021). Thus, later laying eiders would have a reduction in Hg from exogenous sources that contribute to egg development, and subsequently less Hg to influence embryonic development.

Despite the patterns detected in this study, there was a large degree of inter-individual variation in lay date. Thus, the mechanisms involved in contributing to inter-individual variation in lay date are an avenue of further investigation regarding how multiple interacting cues/stressors may influence variation in laying phenology (e.g., Love et al., 2010). This is especially true in a continually warming Arctic which is starting to relieve phenological constraints on individuals to gather enough body stores and reach threshold body conditions needed to lay and incubate successfully (Hanssen et al., 2002; Love et al., 2010). However, while increased colony-wide breeding potential may initially seem beneficial, this outcome may present complications in successive reproductive stages such as incubation and brood rearing.

4.2. Impact of multiple stressor exposure on incubation interruptions

While warmer spring weather provides benefits via greater breeding opportunities for a larger number of females (see above), these results show that exposure to higher temperatures can also have negative impacts on incubation behaviour, with potential downstream consequences on overall reproductive success. In a warm year, females in lower body condition have a greater probability of initiating breeding in this colony (Love et al., 2010). However, the results show that incubating females facing warmer conditions, and those exposed to lower wind speeds, had more frequent interruptions during earlier stages of incubation, potentially due to lower levels of investment in nest outcome through decreased PRL concentrations, the release of excess heat from the nest, or a greater need for recesses to obtain water (Bourgeon et al., 2006; Tartu et al., 2016; DuRant et al., 2019). Specifically, females that move more on the nest, possibly due to difficulty with body or nest temperature regulation, or increased recesses to obtain water as a result of increased nest level air temperature and lower winds, could be more susceptible to depletion of stored resources during the incubation fast (Hanssen et al., 2002; Bottitta et al., 2003; Sénéchal et al., 2011). Further, greater nest movements may put females at a higher risk of attracting more attention from predators such as gulls, arctic foxes (*Vulpes lagopus*), and polar bears (Smith et al., 2012; Jagielski et al., 2021). In the case of high wind speeds where movements were shown to decrease, females may remain still to avoid detection from gulls taking advantage of windy conditions (Gilchrist and Gaston, 1997; Gilchrist et al., 1998; Allard, 2006). Furthermore, preliminary investigations at the East Bay Island colony suggest that the foraging success of polar bears is partially due to on-nest eider movements attracting bears to their nest locations (Geldart, 2021). While we were unable to account for the effect of bear presence on eider incubation due to the lack of certainty in comprehensive island-wide video data, our research demonstrates that future studies on the connection between multiple stressors, incubation behaviour and predation risk, represents an important avenue for future investigation, particularly given the increasing predation pressures some seabirds are concurrently facing (Noyes et al., 2009; Smith et al., 2010; Kimberly and Salice, 2013; Iverson et al., 2014; Prop et al., 2015).

The interactive effect of temperature and THg concentrations on incubation behaviour demonstrated that at higher temperatures, individuals with greater THg concentrations had less movements than those with lower THg concentrations. The prediction was that higher THg concentrations would result in greater movements due to reductions in PRL that may negatively impact incubation consistency (Tartu et al., 2015, 2016). However, in this study, the combination of THg and heat stressors resulted in less incubation interruptions, potentially due to a more complex system than anticipated that includes the reaction of females to acute heat stress, as well as the suppressing effect of THg on CORT, which in-turn may interact with PRL concentrations (Provencher et al., 2016; Tartu et al., 2015, 2016; Choy et al., 2021). Females with lower THg concentrations may have a heightened acute stress response to heat exposure outside of their thermal limits, releasing CORT that suppresses PRL and results in greater incubation interruptions (Tartu et al., 2015, 2016; Choy et al., 2021). While this action is a potential self-preservation method to obtain water and prevent dehydration, the female risks egg overheating and greater predation risk due to female absence and movements attracting predators (Smith et al., 2012; Geldart, 2021; Ridley et al., 2021). Meanwhile, females with higher THg concentrations may reduce this stress response, thus resulting in fewer incubation interruptions, but which have the potential to risk greater water loss and dehydration, thus higher mass loss that may be detrimental to female health (Parker and Holm, 1990; Ridley et al., 2021). However, these mechanistic linkages between THg, CORT and PRL have not been tested in relation to heat stressors and represent a complex system that is of future research interest due to the potential impacts on incubation duration, endogenous resource mobilization rates and dehydration, and predation risk (Olson et al., 2006; Hart et al., 2016; Høyvik Hilde et al., 2016). Additionally, THg and low CORT have been linked with weaker immune systems, higher oxidative stress, and greater lipid metabolism rates, which may cumulatively put female eider endogenous resource stores and overall health at greater risk (Fallacara et al., 2011; Whitney and Cristol, 2017; Vagasi et al., 2018). Therefore, the deleterious effects of THg on the female immune system and metabolic rates, coupled with the reported positive effect of higher CORT on immune system response and reduced oxidative damage (Vagasi et al., 2018), may also be further complex, yet key factors that influence her incubation behaviour, especially in stressful thermal environments.

Overall, the combined effect of offspring THg concentrations, along with inconsistent incubation temperatures influenced by changes in incubation behaviour, may have long-term negative impacts on female health metrics, offspring recruitment and long-term population persistence. To better corroborate these relationships, future studies should collect blood samples from incubating birds to explore the relationship between circulating THg and CORT concentrations as well as body mass loss on incubation behaviour. Our project suggests that future research would be able to obtain a more holistic conclusion by incorporating these internal mechanisms, in addition to nest-level air temperatures and wind speeds, all of which have the potential to reduce the benefits of earlier laying and increased breeding propensity associated with warmer springs.

5. Conclusion

Arctic seabird colonies are being exposed to increasingly warming conditions and the effects of contaminants (Muir et al., 1999; Macdonald et al., 2000; Dietz et al., 2009; Mallory and Braune, 2012; Foster et al., 2019). Higher air temperatures, in combination with lower THg concentrations, were correlated with laying phenology and decreased incubation interruptions in female common eiders. These results demonstrate that even sub-lethal THg concentrations (considered low) can have negative downstream consequences on incubation consistency when females are breeding under elevated air temperatures. These effects are expected to subsequently generate impacts on reproductive success and female health. Taken together, these combined results show it is important to examine the full suite of benefits and costs that climate change may generate for marine birds such as eiders at all stages of reproduction. Overall, interactive effects of multiple stressor exposure are an increasingly important research avenue due to the potential implications on reproductive success and, in the long-term, offspring recruitment and colony subsistence.

CRediT authorship contribution statement

Reyd A. Smith: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Saya S. Albonaimi:** Validation, Writing – review & editing. **Holly L. Hennin:** Conceptualization, Investigation, Writing – review & editing. **H. Grant Gilchrist:** Conceptualization, Project administration, Writing – review & editing. **Jérôme Fort:** Resources, Writing – review & editing. **Kyle J.L. Parkinson:** Conceptualization, Writing – review & editing. **Jennifer F. Provencher:** Conceptualization, Writing – review & editing. **Oliver P. Love:** Supervision, Methodology, Project administration, 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.

Acknowledgments

Thank you to the East Bay Island and Mainland crews in 2018 and 2019 who assisted in data collection, and Maud Brault-Favrou and the Isotopic Spectrometry Facility at LIENSs (La Rochelle University - CNRS, La Rochelle) for their help with sample analysis. We also thank Environment and Climate Change Canada (ECCC), the Natural Sciences and Engineering Research Council of Canada, Canada Research Chairs Program, the Nunavut Wildlife Research Trust, Northern Scientific Training Program, Polar Continental Shelf Project, POLAR Canada, the Canadian Network of Centres of Excellence (ArcticNet), the American Ornithological Society, the Government of Ontario, the University of Windsor and the Arctic Institute of North America for logistical support, research and/or personal funding. This work is also a contribution to the to the ARCTIC-STRESSORS project (ANR-20-CE34-0006-01). Animal care approval for this project was granted through the University of Windsor Committee for Animal Care (AUPP #11-06) and ECCC Animal Care (EC-PN-15-026).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150882.

References

Ackerman, J.T., Herzog, M.P., Schwarzbach, S.E., 2013. Methylmercury is the predominant form of mercury in bird eggs: a synthesis. Environmental science & Technology 47 (4), 2052–2060.

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., Peterson, S.H., Evers, D.C., Jackson, A.K., Elliott, J.E., Vander Pol, S.S., Bryan, C.E., 2016a. Avian mercury exposure and toxicological risk across western North America: a synthesis. Sci. Total Environ. 568, 749–769.

Ackerman, J.T., Eagles-Smith, C.A., Herzog, M.P., Hartman, C.A., 2016b. Maternal transfer of contaminants in birds: mercury and selenium concentrations in parents and their eggs. Environ. Pollut. 210, 145–154.

Adlard, B., Donaldson, S.G., Odland, J.O., Weihe, P., Berner, J., Carlsen, A., Bonefeld-Jorgensen, E.C., Dudarev, A.A., Gibson, J.C., Krümmel, E.M., Ólafsdóttir, K., 2018. Future directions for monitoring and human health research for the Arctic monitoring and assessment programme. Glob. Health Action 11 (1), 1480084.

Akearok, J.A., Hebert, C.E., Braune, B.M., Mallory, M.L., 2010. Inter-and intraclutch variation in egg mercury levels in marine bird species from the Canadian Arctic. Sci. Total Environ. 408 (4), 836–840.

Albers, P.H., Koterba, M.T., Rossmann, R., Link, W.A., French, J.B., Bennett, R.S., Bauer, W.C., 2007. Effects of methylmercury on reproduction in American kestrels. Environmental Toxicology and Chemistry: An International Journal 26 (9), 1856–1866.

Allard, K.A., 2006. Foraging Ecology of an Avian Predator, the Herring Gull. School of Biological Sciences, University of East Anglia Doctoral dissertation.

AMAP, 2021. Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Amélineau, F., Grémillet, D., Harding, A.M., Walkusz, W., Choquet, R., Fort, J., 2019. Arctic climate change and pollution impact little auk foraging and fitness across a decade. Sci. Rep. 9 (1), 1–15.

Andersen, J.H., Berzaghi, F., Christensen, T., Geertz-Hansen, O., Mosbech, A., Stock, A., Zinglersen, K.B., Wisz, M.S., 2017. Potential for cumulative effects of human stressors on fish, sea birds and marine mammals in Arctic waters. Estuar. Coast. Shelf Sci. 184, 202–206.

Angelier, F., Wingfield, J.C., Tartu, S., Chastel, O., 2016. Does prolactin mediate parental and life-history decisions in response to environmental conditions in birds? A review. Horm. Behav. 77, 18–29.

Bårdsen, B.J., Hanssen, S.A., Bustnes, J.O., 2018. Multiple stressors: modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird. Ecosphere 9 (7), e02342.

Bodner, T.E., 2017. Standardized effect sizes for moderated conditional fixed effects with continuous moderator variables. Front. Psychol. 8, 562.

Borgå, K., 2019. The Arctic ecosystem: a canary in the coal mine for global multiple stressors. Environ. Toxicol. Chem. 38 (3), 487–488.

Bottitta, G.E., Nol, E., Gilchrist, H.G., 2003. Effects of experimental manipulation of incubation length on behavior and body mass of common eiders in the Canadian Arctic. Waterbirds 26 (1), 100–107.

Bourgeon, S., Raclot, T., 2006. Corticosterone selectively decreases humoral immunity in female eiders during incubation. J. Exp. Biol. 209 (24), 4957–4965.

Bourgeon, S., Raclot, T., 2007. Triiodothyronine suppresses humoral immunity but not T-cell-mediated immune response in incubating female eiders (Somateria mollissima). Gen. Comp. Endocrinol. 151 (2), 188–194.

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 (5), 358–363.

Brasso, R.L., Abdel Latif, M.K., Cristol, D.A., 2010. Relationship between laying sequence and mercury concentration in tree swallow eggs. Environ. Toxicol. Chem. 29 (5), 1155–1159.

Bustnes, J.O., Bakken, V., Erikstad, K.E., Mehlum, F., Skaare, J.U., 2001. Patterns of incubation and nest-site attentiveness in relation to organochlorine (PCB) contamination in glaucous gulls. J. Appl. Ecol. 38 (4), 791–801.

Bustnes, J.O., Moe, B., Herzke, D., Hanssen, S.A., Nordstad, T., Sagerup, K., Gabrielsen, G.W., Borgå, K., 2010. Strongly increasing blood concentrations of lipid-soluble organochlorines in high arctic common eiders during incubation fast. Chemosphere 79 (3), 320–325.

Camfield, A., Martin, K., 2009. The influence of ambient temperature on horned lark incubation behaviour in an alpine environment. Behaviour 146 (12), 1615–1633.

Choy, E.S., O'Connor, R.S., Gilchrist, H.G., Hargreaves, A.L., Love, O.P., Vézina, F., Elliott, K.H., 2021. Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. J. Exp. Biol. 224 (13), p.jeb242168.

Clayden, M.G., Arsenault, L.M., Kidd, K.A., O'Driscoll, N.J., Mallory, M.L., 2015. Mercury bioaccumulation and biomagnification in a small Arctic polynya ecosystem. Sci. Total Environ. 509, 206–215.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences. Lawrence Erlbaum, Hillsdale, NJ.

Conway, C.J., Martin, T.E., 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54 (2), 670–685.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11 (12), 1304–1315.

D'Alba, L., Monaghan, P., Nager, R.G., 2009. Thermal benefits of nest shelter for incubating female eiders. J. Therm. Biol. 34 (2), 93–99.

Descamps, S., Bêty, J., Love, O.P., Gilchrist, H.G., 2011. Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. Funct. Ecol. 25 (3), 671–681.

Descamps, S., Aars, J., Fuglei, E., Kovacs, K.M., Lydersen, C., Pavlova, O., Pedersen, Å.Ø., Ravolainen, V., Strøm, H., 2017. Climate change impacts on wildlife in a high Arctic archipelago–Svalbard Norway. 23 (2), 490–502.

Dietz, R., Outridge, P.M., Hobson, K.A., 2009. Anthropogenic contributions to mercury levels in present-day Arctic animals—a review. Sci. Total Environ. 407 (24), 6120–6131.

Durant, S.E., Hepp, G.R., Moore, I.T., Hopkins, B.C., Hopkins, W.A., 2010. Slight differences in incubation temperature affect early growth and stress endocrinology of wood duck (Aix sponsa) ducklings. J. Exp. Biol. 213 (1), 45–51.

DuRant, S.E., Willson, J.D., Carroll, R.B., 2019. Parental effects and climate change: will avian incubation behavior shield embryos from increasing environmental temperatures? Integr. Comp. Biol. 59 (4), 1068–1080.

El Halawani, M.E., Burke, W.H., Millam, J.R., Fehrer, S.C., Hargis, B.M., 1984. Regulation of prolactin and its role in gallinaceous bird reproduction. J. Exp. Zool. 232 (3), 521–529.

Erikstad, K.E., Tveraa, T., Bustnes, J.O., 1998. Significance of intraclutch egg-size variation in common eider: the role of egg size and quality of ducklings. J. Avian Biol. 29, 3–9.

Evers, D.C., Taylor, K.M., Major, A., Taylor, R.J., Poppenga, R.H., Scheuhammer, A.M., 2003. Common loon eggs as indicators of methylmercury availability in North America. Ecotoxicology 12 (1–4), 69–81.

Fallacara, D.M., Halbrook, R.S., French, J.B., 2011. Toxic effects of dietary methylmercury on immune system development in nestling american kestrels (Falco sparverius). Environ. Toxicol. Chem. 30 (6), 1328–1337.

Fast, P.L., Gilchrist, H.G., Clark, R.G., 2007. Experimental evaluation of nest shelter effects on weight loss in incubating common eiders Somateria mollissima. J. Avian Biol. 38 (2), 205–213.

Fort, J., Robertson, G.J., Grémillet, D., Traisnel, G., Bustamante, P., 2014. Spatial ecotoxicology: migratory Arctic seabirds are exposed to mercury contamination while overwintering in the Northwest Atlantic. Environ. Sci. Technol. 48 (19), 11560–11567.

Foster, K.L., Braune, B.M., Gaston, A.J., Mallory, M.L., 2019. Climate influence on mercury in Arctic seabirds. Sci. Total Environ. 693, 133569.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., Wanless, S., 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J. Anim. Ecol. 75 (6), 1259–1268.

Garbus, S.E., Lyngs, P., Thyme, A.P., Christensen, J.P., Sonne, C., 2018. Candling and field atlas of early egg development in common eiders Somateria mollissima in the Central Baltic. Acrocephalus 39 (178–179), 85–90.

Geldart, E.A., 2021. Assessing the Adaptive Capacity of an Arctic Seabird to Increasing Frequency in Predation Risk from Polar Bears Using Behavioural and Physiological Metrics. Masters Thesis, University of Windsor, Canada.

Gilchrist, H.G., Gaston, A.J., 1997. Effects of murre nest site characteristics and wind conditions on predation by glaucous gulls. Can. J. Zool. 75 (4), 518–524.

Gilchrist, H.G., Gaston, A.J., Smith, J.N., 1998. Wind and prey nest sites as foraging constraints on an avian predator, the glaucous gull. Ecology 79 (7), 2403–2414.

Gundersen, C.B., Braaten, H.F.V., Steindal, E.H., Moe, S.J., Yakushev, E., Christensen, G., Kirk, J., Hintelmann, H., Frolova, N., Terentjev, P., Roberts, S., 2020. Mercury Risk Evaluation, Risk Management and Risk Reduction Measures in the Arctic (ARCRISK)–Inception Report. NIVA-rapport.

Hallinger, K.K., Cristol, D.A., 2011. The role of weather in mediating the effect of mercury exposure on reproductive success in tree swallows. Ecotoxicology 20 (6), 1368–1377.

Hanssen, S., Engebretsen, H., Erikstad, K., 2002. Incubation start and egg size in relation to body reserves in the common eider. Behav. Ecol. Sociobiol. 52 (4), 282–288.

Hanssen, S.A., Hasselquist, D., Folstad, I., Erikstad, K.E., 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proc. R. Soc. B Biol. Sci. 272 (1567), 1039–1046.

Hart, L.A., Downs, C.T., Brown, M., 2016. Sitting in the sun: nest microhabitat affects incubation temperatures in seabirds. J. Therm. Biol. 60, 149–154.

Hawkings, J.R., Linhoff, B.S., Wadham, J.L., Stibal, M., Lamborg, C.H., Carling, G.T., Lamarche-Gagnon, G., Kohler, T.J., Ward, R., Hendry, K.R., Falteisek, L., 2021. Large subglacial source of mercury from the southwestern margin of the Greenland ice sheet. Nat. Geosci. 1–7.

Hebert, C.E., Chételat, J., Beck, R., Dolgova, S., Fordy, K., Kirby, P., Martin, P., Rabesca, M., 2021. Inter-annual variation of mercury in aquatic bird eggs and fish from a large subarctic lake under a warming climate. Sci. Total Environ. 766, 144614.

Hennin, H.L., Legagneux, P., Bêty, J., Williams, T.D., Gilchrist, H.G., Baker, T.M., Love, O.P., 2015. Pre-breeding energetic management in a mixed-strategy breeder. Oecologia 177 (1), 235–243.

Hennin, H.L., Dey, C.J., Bêty, J., Gilchrist, H.G., Legagneux, P., Williams, T.D., Love, O.P., 2018. Higher rates of prebreeding condition gain positively impacts clutch size: a mechanistic test of the condition-dependent individual optimization model. Funct. Ecol. 32 (8), 2019–2028.

Higgott, C.G., Evans, K.L., Hatchwell, B.J., 2020. Incubation in a temperate passerine: do environmental conditions affect incubation period duration and hatching success? Front. Ecol. Evol. 8, 318.

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science 328 (5985), 1523–1528.

Høyvik Hilde, C., Pélabon, C., Guéry, L., Gabrielsen, G.W., Descamps, S., 2016. Mind the wind: microclimate effects on incubation effort of an arctic seabird. Ecol. Evol. 6 (7), 1914–1921.

Iverson, S.A., Gilchrist, H.G., Smith, P.A., Gaston, A.J., Forbes, M.R., 2014. Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. Proc. R. Soc. B Biol. Sci. 281 (1779), 20133128.

Jagielski, P.M., Dey, C.J., Gilchrist, H.G., Richardson, E.S., Love, O.P., Semeniuk, C.A., 2021. Polar bears are inefficient predators of seabird eggs. R. Soc. Open Sci. 8 (4), 210391.

Jean-Gagnon, F., Legagneux, P., Gilchrist, G., Bélanger, S., Love, O.P., Bêty, J., 2018. The impact of sea ice conditions on breeding decisions is modulated by body condition in an arctic partial capital breeder. Oecologia 186 (1), 1–10.

Jenssen, B.M., 2006. Endocrine-disrupting chemicals and climate change: a worst-case combination for arctic marine mammals and seabirds? Environ. Health Perspect. 114 (Suppl. 1), 76–80.

Kilpi, M., Lindström, K., 1997. Habitat-specific clutch size and cost of incubation in common eiders Somateria mollissima. 111 (3), 297–301.

Kimberly, D.A., Salice, C.J., 2013. Interactive effects of contaminants and climate-related stressors: high temperature increases sensitivity to cadmium. Environ. Toxicol. Chem. 32 (6), 1337–1343.

Kirk, J.L., Lehnherr, I., Andersson, M., Braune, B.M., Chan, L., Dastoor, A.P., Durnford, D., Gleason, A.L., Loseto, L.L., Steffen, A., Louis, V.L.S., 2012. Mercury in Arctic marine ecosystems: sources, pathways and exposure. Environ. Res. 119, 64–87.

Le Bohec, C., Whittington, J.D., Le Maho, Y., 2013. Polar monitoring: seabirds as sentinels of marine ecosystems. Adaptation and Evolution in Marine Environments. Volume 2. Springer, Berlin, Heidelberg, pp. 205–230.

Lewis, K.M., van Dijken, G.L., Arrigo, K.R., 2020. Changes in phytoplankton concentration now drive increased Arctic Ocean primary production. Science 369 (6500), 198–202.

Long, J.A., 2019. Interactions: Comprehensive, User-Friendly Toolkit for Probing Interactions. R package version 1.1.0. . https://cran.r-project.org/package=interactions.

Love, O.P., Gilchrist, H.G., Descamps, S., Semeniuk, C.A., Bêty, J., 2010. Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. Oecologia 164 (1), 277–286.

Macdonald, R.W., Barrie, L.A., Bidleman, T.F., Diamond, M.L., Gregor, D.J., Semkin, R.G., Strachan, W.M.J., Li, Y.F., Wania, F., Alaee, M., Alexeeva, L.B., 2000. Contaminants in the Canadian Arctic: 5 years of progress in understanding sources, occurrence and pathways. Sci. Total Environ. 254 (2–3), 93–234.

Mallory, M.L., Braune, B.M., 2012. Tracking contaminants in seabirds of Arctic Canada: temporal and spatial insights. Mar. Pollut. Bull. 64 (7), 1475–1484.

Martin, K., Wiebe, K.L., 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. Integr. Comp. Biol. 44 (2), 177–185.

Mallory, M.L., Gaston, A.J., Gilchrist, H.G., Robertson, G.J., Braune, B.M., 2010. Effects of climate change, altered sea-ice distribution and seasonal phenology on marine birds. A Little less Arctic. Springer, Dordrecht, pp. 179–195.

Martin, T.E., Oteyza, J.C., Boyce, A.J., Lloyd, P., Ton, R., 2015. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. Am. Nat. 186 (2), 223–236.

McPartland, M., Garbus, S.E., Lierhagen, S., Sonne, C., Krøkje, Å., 2020. Lead isotopic signatures in blood from incubating common eiders (Somateria mollissima) in the Central Baltic Sea. Environ. Int. 142, 105874.

Møller, A.P., Fiedler, W., Berthold, P. (Eds.), 2010. Effects of Climate Change on Birds. OUP Oxford.

Muir, D., Braune, B., DeMarch, B., Norstrom, R., Wagemann, R., Lockhart, L., Hargrave, B., Bright, D., Addison, R., Payne, J., Reimer, K., 1999. Spatial and temporal trends and effects of contaminants in the Canadian Arctic marine ecosystem: a review. Sci. Total Environ. 230 (1–3), 83–144.

Nord, A., Nilsson, J.Å., 2011. Incubation temperature affects growth and energy metabolism in blue tit nestlings. Am. Nat. 178 (5), 639–651.

Noyes, P.D., McElwee, M.K., Miller, H.D., Clark, B.W., Van Tiem, L.A., Walcott, K.C., Erwin, K.N., Levin, E.D., 2009. The toxicology of climate change: environmental contaminants in a warming world. Environ. Int. 35 (6), 971–986.

Olson, C.R., Vleck, C.M., Vleck, D., 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. Physiol. Biochem. Zool. 79 (5), 927–936.

Parker, H., Holm, H., 1990. Patterns of nutrient and energy expenditure in female common eiders nesting in the high arctic. The Auk 107 (4), 660–668.

Piatt, J.F., Sydeman, W.J., Wiese, F., 2007. Introduction: a modern role for seabirds as indicators. Mar. Ecol. Prog. Ser. 352, 199–204.

Pollet, I.L., Leonard, M.L., O'Driscoll, N.J., Burgess, N.M., Shutler, D., 2017. Relationships between blood mercury levels, reproduction, and return rate in a small seabird. Ecotoxicology 26 (1), 97–103.

Pratte, I., Braune, B.M., Hobson, K.A., Mallory, M.L., 2019. Variable Sea-ice conditions influence trophic dynamics in an Arctic community of marine top predators. Ecol. Evol. 9 (13), 7639–7651.

Prop, J., Aars, J., Bårdsen, B.J., Hanssen, S.A., Bech, C., Bourgeon, S., de Fouw, J., Gabrielsen, G.W., Lang, J., Noreen, E., Oudman, T., 2015. Climate change and the increasing impact of polar bears on bird populations. Front. Ecol. Evol. 3, 33.

Provencher, J.F., Mallory, M.L., Braune, B.M., Forbes, M.R., Gilchrist, H.G., 2014. Mercury and marine birds in Arctic Canada: effects, current trends, and why we should be paying closer attention. Environ. Rev. 22 (3), 244–255.

Provencher, J.F., Forbes, M.R., Hennin, H.L., Love, O.P., Braune, B.M., Mallory, M.L., Gilchrist, H.G., 2016. Implications of mercury and lead concentrations on breeding physiology and phenology in an Arctic bird. Environ. Pollut. 218, 1014–1022.

Reiter, M.E., Andersen, D.E., 2008. Comparison of the egg flotation and egg candling techniques for estimating incubation day of Canada goose nests. J. Field Ornithol. 79 (4), 429–437.

Renaut, S., Devred, E., Babin, M., 2018. Northward expansion and intensification of phytoplankton growth during the early ice-free season in Arctic. Geophys. Res. Lett. 45 (19), 10590–10598.

Ridley, A.R., Wiley, E.M., Bourne, A.R., Cunningham, S.J., Nelson-Flower, M.J., 2021. Understanding the potential impact of climate change on the behavior and demography of social species: the pied babbler (Turdoides bicolor) as a case study. Adv. Study Behav. 53, 225–266.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1 (2), 103–113.

Schindler, D.W., Smol, J.P., 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. AMBIO: a Journal of the Human Environment 35 (4), 160–168.

Schuster, P.F., Schaefer, K.M., Aiken, G.R., Antweiler, R.C., Dewild, J.F., Gryziec, J.D., Gusmeroli, A., Hugelius, G., Jafarov, E., Krabbenhoft, D.P., Liu, L., 2018. Permafrost stores a globally significant amount of mercury. Geophys. Res. Lett. 45 (3), 1463–1471.

Sénéchal, É., Bêty, J., Gilchrist, H.G., Hobson, K.A., Jamieson, S.E., 2011. Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. Oecologia 165 (3), 593–604.

Smith, P.A., Elliott, K.H., Gaston, A.J., Gilchrist, H.G., 2010. Has early ice clearance increased predation on breeding birds by polar bears? Polar Biol. 33 (8), 1149–1153.

Smith, P.A., Tulp, I., Schekkerman, H., Gilchrist, H.G., Forbes, M.R., 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. Anim. Behav. 84 (4), 835–842.

Smith, R.A., Yurkowski, D.J., Parkinson, K.J.L., Fort, J., Hennin, H.L., Gilchrist, H.G., Hobson, K.A., Mallory, M.L., Danielsen, J., Garbus, S., Hanssen, S.A., Jónsson, J.E., Latty, C.J., Moe, B., Parsons, G.J., Sonne, C., Tertitski, G., Love, O.P., 2021. Environmental and life-history factors influencing inter-colony and multidimensional niche metrics of breeding common eider. Sci. Total Environ. 796, 148935.

Swennen, C., Van der Meer, J., 1995. Composition of eggs of common eiders. Can. J. Zool. 73 (3), 584–588.

Tartu, S., Goutte, A., Bustamante, P., Angelier, F., Moe, B., Clément-Chastel, C., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2013. To breed or not to breed: endocrine response to mercury contamination by an Arctic seabird. Biol. Lett. 9 (4), 20130317.

Tartu, S., Bustamante, P., Goutte, A., Cherel, Y., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2014. Age-related mercury contamination and relationship with luteinizing hormone in a long-lived Antarctic bird. PLoS One 9 (7), e103642.

Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2015. Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. Sci. Total Environ. 505, 180–188.

Tartu, S., Bustamante, P., Angelier, F., Lendvai, A.Z., Moe, B., Blévin, P., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2016. Mercury exposure, stress and prolactin secretion in an Arctic seabird: an experimental study. Funct. Ecol. 30 (4), 596–604.

Timmermans, M.L., Proshutinsky, A., Krishfield, R.A., Perovich, D.K., Richter-Menge, J.A., Stanton, T.P., Toole, J.M., 2011. Surface freshening in the Arctic Ocean's Eurasian Basin: an apparent consequence of recent change in the wind-driven circulation. J. Geophys. Res. Ocean 116 (C8).

Vagasi, C.I., Pătraş, L., Pap, P.L., Vincze, O., Mureşan, C., Nemeth, J., Lendvai, A.Z., 2018. Experimental increase in baseline corticosterone level reduces oxidative damage and enhances innate immune response. PLoS One 13 (2), e0192701.

Vinebrooke, D.R., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., C. Maberly, S.C., Sommer, U., 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos 104 (3), 451–457.

Visser, M.E., Holleman, L.J., Caro, S.P., 2009. Temperature has a causal effect on avian timing of reproduction. Proc. R. Soc. B Biol. Sci. 276 (1665), 2323–2331.

Wassmann, P., Duarte, C.M., Agusti, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. Glob. Chang. Biol. 17 (2), 1235–1249.

Wayland, M., Gilchrist, H.G., Neugebauer, E., 2005. Concentrations of cadmium, mercury and selenium in common eider ducks in the eastern Canadian arctic: influence of reproductive stage. Sci. Total Environ. 351, 323–332.

Whitney, M.C., Cristol, D.A., 2017. Impacts of sublethal mercury exposure on birds: a detailed review. Reviews of Environmental Contamination and Toxicology. Springer, Cham, pp. 113–163.

Zhang, J., 2005. Warming of the arctic ice-ocean system is faster than the global average since the 1960s. Geophys. Res. Lett. 32 (19).