

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

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8 **Abstract**

9 Wildlife are exposed to multiple stressors across life history stages, the effects of which can be  
10 amplified as human activity surges globally. In Arctic regions, increasing air and ocean  
11 temperatures, more severe weather systems, and exposure to environmental contaminants all  
12 represent stressors occurring simultaneously. While Arctic vertebrates, including marine birds,  
13 are expected to be at risk of adverse effects from these individual stressors, few studies have  
14 researched their combined impacts on breeding behaviour and reproductive success. We  
15 examined the interactive effects of environmental conditions and mercury (Hg) contamination on  
16 laying phenology and incubation behaviour in female common eiders (*Somateria mollissima*,  
17 Mitiq) nesting at Canada's largest Arctic breeding colony. Exposure to higher pre-breeding air  
18 temperatures were linked to females with higher egg Hg levels laying earlier than those with  
19 lower Hg levels. Furthermore, examination of a total of 190 days of incubation behaviour from  
20 61 eiders across two years revealed a negative relationship between wind speed and the  
21 frequency of incubation interruptions. Importantly, exposure to higher air temperatures combined  
22 with lower Hg levels was significantly correlated with increased incubation interruptions.  
23 Although previous research has shown that warmer spring temperatures could afford lower  
24 quality females more time to improve body condition to successfully lay, our results suggest  
25 these females may face stronger cumulative fitness costs during incubation in warmer years,

26 potentially in combination with the effects of Hg on physiological stress and hormone secretion.  
27 This study highlights how multiple stressors exposure, driven by human-induced environmental  
28 changes, can have a complex influence on reproduction.

29

30 **Keywords:** multiple stressors; mercury; climate change; common eider; physiology

### 31 **1. Introduction**

32 Climate change is shifting environmental conditions in Arctic regions through expansive  
33 reductions in sea ice cover, increased frequency, severity, and unpredictability of extreme  
34 climatic events, and elevated air temperatures three times the global average (Zhang 2005;  
35 Hoegh-Guldberg and Bruno 2010; Timmermans et al. 2011; AMAP 2021). These climatic  
36 alterations have the potential to affect Arctic species, with effects ranging from changes in  
37 primary productivity abundance and phenology, to alterations in prey availability for top marine  
38 and terrestrial predators in a complex, connected system (Frederiksen et al. 2006; Renaut et al.  
39 2018; Pratte et al. 2019; Lewis et al. 2020). Marine birds in particular are known to be highly  
40 sensitive to environmental change and elevated thermal environments (Piatt et al. 2007; Le  
41 Bohec et al. 2013; Choy et al. 2021). Environmental shifts can alter avian migratory and  
42 reproductive phenology, especially in the Arctic which offers a short favorable window for those  
43 breeding, notably via spatio-temporal constraints in prey availability at extreme latitudes (Martin  
44 and Wiebe 2004). Higher air temperatures have been shown to directly impact reproduction by  
45 advancing lay dates, accelerating embryonic growth, and decreasing incubation attentiveness in  
46 birds (Camfield and Martin 2009; Visser et al. 2009; Durant et al. 2010; Nord and Nilsson 2011).  
47 Lowered incubation attentiveness can not only extend the incubation period and potentially  
48 impact successful hatching and fledging through heightened predation risk (Conway and Martin

49 2007; Smith et al. 2012; Higgott et al. 2020), but it can also leave the female in worse body  
50 condition relative to females with lower incubation effort through increased time spent  
51 maintaining optimal clutch temperature (Bottitta et al. 2003; D’Alba et al. 2009; Høyvik Hilde et  
52 al. 2016). In relation to thermal conditions, higher wind speeds can result in increased incubation  
53 effort and higher body mass loss (Kilpi and Lindstrom 1997; Høyvik Hilde et al. 2016). In  
54 contrast, low wind speeds when combined with high temperatures can instead exacerbate  
55 incubation effort due to birds exceeding their thermal neutral zones (Fast et al. 2007), with  
56 downstream negative effects on embryonic development time, egg and duckling predation risk,  
57 therefore risking costs to the female’s fitness (Hanssen et al. 2005; Martin et al. 2015).

58         While the impacts of climate change on Arctic species are well appreciated (Møller et al.  
59 2010; Wassmann et al. 2010; Descamps et al. 2017), these ecosystems now face many additional  
60 and simultaneous environmental stressors. Many contaminants exist in the Arctic in relatively  
61 high concentrations from long-range transport towards the poles by air and ocean currents, as  
62 well as via the melting of permafrost and glaciers that release contaminants stored from decades  
63 of elevated contaminant output (Macdonald et al. 2000; Kirk et al. 2012; Schuster et al. 2018,  
64 Hawkings et al. 2021). Mercury (Hg) has been noted as a research priority in Arctic marine  
65 systems because of its higher rates of contamination relative to terrestrial systems and its toxic  
66 effects across multiple vertebrate taxa (Provencher et al. 2014; Adlard et al. 2018; Gundersen et  
67 al. 2020). In marine birds, Hg contamination even at low levels can have system wide, adverse  
68 effects on neurology, physiology, behaviour, and reproduction (Albers et al. 2007; Ackerman et  
69 al. 2016a; Whitney and Cristol 2017; Pollet et al. 2017). Sub-lethal Hg has been correlated with a  
70 decrease in the likelihood to breed in marine birds, mechanistically linked with reductions in key  
71 reproductive hormones (e.g., luteinizing hormone, estrogens), as well as the growth of gonadal

72 tissues (Tartu et al. 2013; 2014). The effects of Hg exposure can also affect later stages of  
73 breeding through reductions in incubation consistency, measured as the frequency of incubation  
74 interruptions (Bustnes et al. 2001). These effects are likely mediated by the endocrine-disrupting  
75 effect of Hg on prolactin (PRL), a hormone key in forming and maintaining parental attachment  
76 to the nest (El Halawani et al. 1984; Tartu et al. 2015; 2016; Angelier et al. 2016). Overall,  
77 exposure to multiple environmental stressors can have downstream effects on reproductive  
78 success and survival (Bustnes et al. 2001; Visser et al. 2009; Durant et al. 2010; Nord and  
79 Nilsson 2011; Hallinger et al. 2011). As such, accounting for multiple stressors in an interactive  
80 effects framework is now considered vital for determining how individually-mediated processes  
81 will impact population and ecosystem processes (Vinebrooke et al. 2004; Schindler and Smol  
82 2006). However, while the combined effects of these stressors are expected to be a ‘worst-case  
83 scenario’ for Arctic species (Jenssen 2006; Borgå 2019), few studies outside of temperate  
84 systems have been able to examine the cumulative effects of multiple stressors on key  
85 mechanisms driving reproductive performance and fitness (Crain et al. 2008; Andersen et al.  
86 2017; Bårdsen et al. 2018, Amélineau et al. 2019).

87         We examined the interactive effects of environmental conditions and maternal Hg levels  
88 (using first-laid eggs as a proxy) in relation to lay date phenology and incubation behaviour in a  
89 long-lived Arctic-breeding marine bird, common eider (*Somateria mollissima*, Mitiq, hereafter  
90 eiders). Eiders use a capital-income based reproductive strategy by utilizing a combination of  
91 stored fat from the wintering grounds and incoming resources from intensive pre-breeding  
92 foraging during migration and at the breeding site to support reproduction (Sénéchal et al. 2011).  
93 Females that can obtain the needed endogenous stores more quickly are able to lay earlier, invest  
94 in larger clutch sizes, and increase offspring recruitment (Love et al. 2010; Descamps et al. 2011;

95 Hennin et al. 2018). In our first objective, we independently and interactively examined whether  
96 lay date was related to individual air temperature, wind speed exposure as well as egg Hg levels  
97 (a direct proxy for female Hg burden at the time of laying; Evers et al. 2003; Brasso et al. 2010;  
98 Ackerman et al. 2016b). We predicted that lay date would vary between sampling years  
99 potentially due to annual environmental and phenological differences in prey availability. We  
100 also predicted that individuals with higher egg Hg levels, exposure to higher air temperatures and  
101 higher wind speeds would result in later lay dates).

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

118

## 119 **2. Methods**

### 120 *2.1 Study site and data collection*

121 We examined female common eiders nesting at the East Bay Island colony (Mitivik Island,  
122 Nunavut, Canada; 64°02'N, 81°47'W), located within in the Qaqsauqtuuq (East Bay) Migratory  
123 Bird Sanctuary. The study period ranged from late June to mid-July in 2016 (n=13), 2017  
124 (n=12), 2018 (n=46) and 2019 (n=38, total N=109), commencing when females throughout the  
125 colony began incubation. We located active nests using spotting scopes from six observation  
126 blinds distributed across the colony from 2016-2019, with additional nests located  
127 opportunistically in 2018-2019. To quantify nest environmental conditions and incubation  
128 behaviour, in 2018 and 2019 between 1 and 13 days after a female laid her first egg, we deployed  
129 temperature-recording pendants (HOBO Pendant® MX2201 and 64K) ~ 0.5 meters away from  
130 each incubating hen at nest level to quantify ambient air temperature every minute. We also  
131 placed a Kestrel 5500 weather meter approximately three meters off the ground in five dispersed  
132 locations across the colony to collect data on average wind speed each hour. Behaviour  
133 monitoring equipment was placed at each nest, consisting of a nest temperature probe (Tinytag®  
134 Plus 2) and a trail camera (Browning 2018 Strike Force Pro). We placed temperature probes at  
135 the bottom of the nest in the middle of the clutch of eggs to record nest temperature every minute  
136 for the duration of that individual nest's incubation period, providing a proxy of incubation  
137 interruptions given that while hens are sitting on eggs, the nest temperature is higher than  
138 external air temperature. We placed motion-activated trail cameras ~1 meter away from the nest  
139 cup to corroborate incubation interruption data from the temperature probes and, when possible,  
140 determine the cause of nest failure (predation, abandonment). All behaviour and environmental

141 monitoring equipment were left in place to collect data for the duration of incubation (roughly 3  
142 weeks), after which all the equipment was retrieved. From the original 84 nests with monitoring  
143 equipment deployed (in 2018-2019), 61 nests (73%, n=31; 2018, n=30; 2019) had useable data  
144 for analysis, while the remaining 23 nests were unusable due to nest predation by polar bears  
145 (*Ursus maritimus*) and/or gulls (*Larus* species), hen nest abandonment, or removal of the nest  
146 temperature probe by the incubating female (0-3 days post deployment; see *Statistical Analysis*).

## 147 **2.2 Egg mercury analysis**

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

158 We individually thawed first-laid common eider eggs collected from 2016-2019 (see  
159 Study site and data collection) and removed the shells for sub-sampling. We collected a total of  
160 1.5mL of both albumen and yolk samples, placed these into individual cryovials, and then re-  
161 froze samples at -20°C. Cryovials for sample storage were acid-washed for two days using 65%  
162 nitric acid (CAS# 7697-37-2) diluted to 20% concentration with Ultrapure water, then rinsed  
163 three times with Ultrapure water. We rinsed all materials used to dissect eggs with Ultrapure

164 water, followed by acid-washing for 10 minutes to minimize cross-contamination, then another  
165 rinse with Ultrapure water before dissection. We then freeze-dried samples for approximately 72  
166 hours, after which they were ground into a fine, homogenized powder using a metal spatula  
167 cleaned with acetone.

168 Analysis of egg Hg levels were conducted at the Littoral Environment et Sociétés  
169 institute (LIENSs, La Rochelle, France) using the yolk and albumen from each first-laid eider  
170 egg collected across all four sampling years (n = 121). Total Hg (THg) levels were determined in  
171 this study as it has been shown in avian eggs to primarily consist of MeHg (methylmercury), the  
172 most highly toxic and biologically mobile form of Hg (Ackerman et al. 2013). Freeze-dried yolk  
173 and albumen samples were analyzed using an Advanced Hg Analyzer spectrophotometer (Altec  
174 AMA 254) set at a detection limit of 0.10 ng dry weight (dw). The quality control program  
175 included running blanks prior to the analysis, as well as analyzing reference materials from  
176 lobster hepatopancreas (TORT-3) from the National Research Council (NRC), Canada (reference  
177 values were  $0.292 \pm 0.022$   $\mu\text{g/g dw}$  SD, mean measured  $\pm$  SD =  $0.285$   $\mu\text{g/g dw}$ , recovery =  
178 1.69%) every 15 samples. Whole egg THg levels were calculated for each egg from the yolk and  
179 albumen values using a known eider yolk:albumen ratio of 1:1 (yolk\*0.5+albumen\*0.5;  
180 Swennen and Van der Meer 1995). All THg levels are reported in  $\mu\text{g/g dw}$ .

181

## 182 ***2.3 Statistical analyses***

### 183 ***2.3.1 Variation in lay date phenology***

184 Eiders form their eggs during a period of rapid follicle growth (RFG; the initiation of yolk  
185 formation which occurs seven days before laying of the first egg in eiders; Hennin et al. 2015).  
186 Therefore, the initiation of the RFG was calculated using each hen's lay date (lay date – 7 days).



187 We used data on average air temperature and wind speed over the seven days prior to the RFG  
188 initiation period for each female collected by the weather station at Coral Harbour (64°11'N,  
189 83°21'W; 68 km from East Bay) using Environment and Climate Change Canada (ECCC)'s  
190 online database ([https://climate.weather.gc.ca/index\\_e.html](https://climate.weather.gc.ca/index_e.html)). These local temperature and wind  
191 values were then used in the model to represent the pre-breeding environmental conditions.

192 We used data from 2016-2019 inclusive to examine how air temperature, wind speed and  
193 THg levels combined to influence individual lay date. Specifically, we ran a Generalized Linear  
194 Model (GLM) using R version 3.6.2 (R Development Core Team) with ordinal lay date as the  
195 dependent variable. Local air temperature and wind speed during the RFG period as well first  
196 laid egg THg levels were included as independent variables individually and in all possible 2-  
197 way interactions, as well as a 3-way interaction. Sampling year was also included as an  
198 independent continuous variable, since having it as a categorical variable caused model  
199 overfitting. All variables in the interactions were standardized and centered for comparison and  
200 to reduce the misrepresentation of effects and improve interpretability of coefficients (Schielzeth  
201 2010). Year was also included as a fixed variable but excluded from interactions. All  
202 assumptions for a GLM were met by visually inspecting histograms to confirm a normal  
203 distribution of the data, quantile-quantile plots, and residual plots from model outputs, as well as  
204 confirming no multicollinearity between all variables, most notably wind speed and air  
205 temperature ( $r = -0.09$ , variance inflation factor (VIF) = 1.05).

206

### 207 ***2.3.2 Variation in incubation behaviour (nesting disturbances)***

208 We examined incubation behaviour in 2018-2019 by quantifying the number of incubation  
209 interruptions as determined by an abrupt shift in nest temperature, preceded and followed by a

210 period of stationary nest temperature. Two separate viewers initially corroborated the nest  
211 temperature data using video footage from the trail cameras to independently train the viewers on  
212 how to accurately interpret female nest movements using the nest temperature data. This was  
213 followed by determination of incubation interruptions using nest temperature data without  
214 consulting the video footage to make up the final, complete dataset. Recesses away from the nest  
215 were counted as one incubation interruption and validated with associated trail camera footage  
216 when available. Incubation interruptions were determined over two consecutive 24-hour periods  
217 in each third of incubation during early (days 4-7; n=49), middle (days 12-15; n=36), and late  
218 stages (days 18-24; n=10, see Supplemental Materials) whenever available before incubation  
219 termination for each of the 61 nests (Bourgeon et al. 2006). These specific ranges in incubation  
220 day were chosen to obtain the highest sample size for each incubation stage while maintaining a  
221 spread of at least five days between stages for each hen. To account for differences in behaviour  
222 across the day, each 24-hour period was separated into four, 6-hour sections ((0:00-5:59; Section  
223 1, 6:00-11:59; Section 2, 12:00-17:59; Section 3, 18:00-23:59; Section 4; see Supplemental  
224 Materials) and the number of incubation interruptions was determined for each female within  
225 each of these time periods for subsequent analysis.

226 We examined how individual female-specific environmental exposure to wind speeds  
227 individually, as well as air temperature individually and in combination with THg levels, related  
228 to her incubation interruptions. We ran a Generalized Linear Mixed Model (GLMM) examining  
229 whether exposure to multiple stressors influenced incubation interruptions using the square-root  
230 transformed number of incubation interruptions in each section of the day as the dependent  
231 variable. We included average air temperature and wind speed for each of the four sections of the  
232 day and individual whole egg THg levels as independent variables. Additionally, we included the

233 interaction between air temperature and THg levels, which were centered and standardized  
234 (Schielzeth 2010). Interactions involving wind speed were excluded from the final model since  
235 they were not significant and prevented model convergence. Section of the day (1-4), incubation  
236 stage (early, mid, late), and individual ID (0-61) were included as categorical random variables.  
237 Year was removed from this analysis because it explained close to 0% of the variance in the  
238 dependent variable. Further examinations into whether individual incubation interruptions varied  
239 in response to the stage of incubation and section of the day as defined above revealed no  
240 significant correlations, however, they remained important covariates in our model.

241 We then calculated the effect sizes of the statistically significant individual variables and  
242 compared these calculated values to established standards of low (0.2), medium (0.6), and large  
243 (0.8; see Cohen 1998). The effect sizes of statistically significant interactions were calculated  
244 and compared to established values of low (0.4), medium (1.0), and large effects (1.6; Bodner  
245 2017) to further disentangle their impacts on incubation interruptions. All assumptions were met  
246 for the GLMMI by visually inspecting histograms to confirm normal distribution of the data,  
247 quantile-quantile plots, and residual plots from model outputs, determining no overdispersion, as  
248 well as determining a lack of multicollinearity between temperature and wind variables ( $r = -$   
249  $0.07$ ,  $VIF = 1.01$ ). Further, as the correlation coefficient for each interaction does not inform us  
250 of the positive or negative direction for all variables within the interaction, significant interactive  
251 model outputs were separately graphed using the R package Interactions v.1.1.3 (Long 2020).

252

### 253 **3. Results**

#### 254 ***3.1 Relationship between multiple environmental stressor exposure and lay date***

255 First-laid eggs from 2016-2019 had an average THg level of  $0.07 \pm 0.03$   $\mu\text{g/g}$  dry weight (dw) in  
256 yolk (range 0.022-0.191  $\mu\text{g/g}$  dw), and  $2.17 \pm 0.87$   $\mu\text{g/g}$  dw in albumen (range 0.60-5.36  $\mu\text{g/g}$   
257 dw) for all years combined (Table 1). Calculation of egg homogenate from the yolk and albumen  
258 results gave an average of  $1.12 \pm 0.44$   $\mu\text{g/g}$  dw (range 0.31-2.72  $\mu\text{g/g}$  dw; Table 1).

259 Lay date had a positive correlation with sampling year, with a range of 10 days in  
260 average lay date between 2016 and 2019 (Table 2A; Supplemental Materials). Additionally, the  
261 parameter associated with the interaction between air temperature and wind speed was  
262 significant. As both temperature and wind speeds increased, birds had later lay dates (Table 2A;  
263 Figure 1). Furthermore, the interaction between air temperature and THg levels had a significant  
264 relationship with lay date (Table 2A; Figure 1). Specifically, higher air temperatures and lower  
265 THg levels correlated with the latest lay dates (Figure 1). Effect size for air temperature alone  
266 was 1.02, considered a strong effect (Cohen 1998), while the interaction between temperature  
267 and THg was calculated to be 1.11, considered to be a medium interactive effect (Bodner 2017).

268

### 269 ***3.2 Effects of exposure to multiple stressors on incubation interruption***

270 Across all females in 2018 and 2019, incubation interruptions occurred  $25 \pm 6$  times a day (years  
271 combined – see Statistical Analysis section of the Methods), with the most attentive eider having  
272 13 incubation interruptions in one day and the most restless female having 45 incubation  
273 interruptions. During early incubation, interruptions occurred  $26 \pm 6$  times, mid-stage  
274 interruptions occurred  $24 \pm 6$  times, and during late-stage incubation interruptions occurred  $23 \pm$   
275  $6$  times a day.

276 Results indicated that exposure to higher temperatures and low wind speeds was related  
277 to greater incubation disturbances (Table 2). Further, the interaction between higher temperature

278 and lower egg THg levels was marginally significant ( $p = 0.05$ ) and correlated with a greater  
279 number of incubation interruptions (Table 2C, Figure 2). The effect size for temperature  
280 individually was 0.18, and therefore considered a small effect (Cohen 1998). However, the effect  
281 size for the interaction between temperature and THg on incubation interruptions was 0.28,  
282 which although still considered a small effect, was larger than temperature alone (Bodner 2017).

283

#### 284 **4. Discussion**

285 The overall aim of this study was to examine the simultaneous effects of multiple stressors on  
286 common eider reproductive phenology and incubation interruptions by determining how these  
287 factors varied with air temperature, wind speed and THg levels. In the pre-breeding period, local  
288 air temperature, wind speed and egg THg levels all influenced lay date. Temperature had the  
289 strongest singular effect and generated a significant interaction with both wind speed and THg  
290 levels to influence laying date. This suggests that birds with the latest lay dates were associated  
291 with exposure to higher air temperatures individually and in an interaction with higher wind  
292 speeds, as well as in an interaction with lower egg THg levels. Notably, egg THg levels were  
293 above levels seen previously at this site from eggs collected a decade before (2008:  $0.50\mu\text{g/g dw}$ ,  
294 range 0.37-0.58; Akearok et al. 2010). Furthermore, nest-level air temperature and wind speed  
295 during incubation showed the strongest relationship with incubation behaviour itself, with THg  
296 having a marginally significant effect on incubation interruptions in an interaction with air  
297 temperature. These patterns suggest that exposure to lower winds, and higher air temperatures  
298 individually and when combined with lower THg levels were correlated with greater incubation  
299 interruptions. These are some of the first empirical results examining multiple stressor

300 relationships, including interactions between environmental conditions and contaminants, on lay  
301 date phenology and behaviour in a wild bird species.

302

#### 303 ***4.1 Influence of multiple environmental stressor exposure on laying phenology***

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

316       Importantly, the advanced melting of snow and ice due to warmer spring temperatures  
317 may release more THg into the environment that, if coinciding with intensified eider pre-  
318 breeding foraging, could lead to increased THg exposure in eiders preparing to breed  
319 (Macdonald et al. 2000; Kirk et al. 2012; Schuster et al. 2018, Hawkings et al. 2021).

320 Importantly, this link between egg Hg levels and spring freshet has recently been demonstrated  
321 in western Canada in gulls and terns (Hebert 2021). We recognize that in this study system a  
322 time lag may exist between when inorganic Hg, released from melting ice, is converted into

323 MeHg and is then accumulated in birds and may reflect in inter-annual variation in eider Hg  
324 levels (Foster et al. 2019). However, in this study lay date varied significantly with an interaction  
325 between air temperature and THg, where higher air temperatures, together with lower THg  
326 levels, were associated with later laying dates (Figure 1). Although counterintuitive that higher  
327 THg levels were correlated with earlier laying, this trend may be explained by previous research  
328 examining links between THg, corticosterone (CORT, a glucocorticoid stress hormone), body  
329 condition, foraging intensity, and arrival date. In previous studies at East Bay Island, earlier  
330 arriving female eiders, which also lay earlier (Descamps et al. 2011), were found to have lower  
331 CORT levels (Hennin et al. 2015; 2016). Furthermore, research has shown that seabirds with  
332 elevated THg levels also had lower CORT and lowered body condition, likely influenced by the  
333 endocrine disrupting effects of THg (Fort et al. 2014; Provencher et al. 2016). These findings  
334 suggest that higher temperatures may lead to greater foraging opportunities due to earlier sea ice  
335 melt, ultimately allowing for more quickly improved body condition and less associated  
336 energetic stress. Thus, birds with greater THg levels may be at a disadvantage due to a further  
337 reduction in CORT that prevents more rapidly improved body condition through reduced  
338 foraging effort. Moreover, eiders at East Bay are known to shift prey selection along with laying  
339 phenology, with birds laying later utilizing bivalves as a prey source, compared to amphipods by  
340 those eiders laying earlier (Sénéchal et al. 2011). This prey shift apparently occurs as sea ice  
341 break-up makes benthic feeding areas increasingly accessible to diving eider ducks (Sénéchal et  
342 al. 2011). Since prey choice and primary production conditions are known to influence eider Hg  
343 levels, eiders that rely on lower trophic level bivalves rather than higher trophic level amphipods  
344 may accumulate less Hg (Mallory et al. 2010b; Clayden et al. 2015; Smith et al. 2021). Thus,  
345 later laying eiders would have a reduction in Hg from exogenous sources that contribute to egg

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

356

#### 357 ***4.2 Impact of multiple stressor exposure on incubation interruptions***

358 While warmer spring weather provides benefits via greater breeding opportunities for a larger  
359 number of females (see above), our results show that exposure to higher temperatures can also  
360 have negative impacts on incubation behaviour, with potential downstream consequences on  
361 overall reproductive success. In a warm year, females in lower body condition have a greater  
362 probability of initiating breeding in this colony (Love et al. 2010). However, our results show  
363 that incubating females facing warmer conditions, and those exposed to lower wind speeds, had  
364 more frequent interruptions during earlier stages of incubation, potentially due to lower levels of  
365 investment in nest outcome through decreased PRL levels, the release of excess heat from the  
366 nest, or greater need for recesses to obtain water (Bourgeon et al. 2006; Tartu et al. 2016;  
367 DuRant et al. 2019). Specifically, females that move more on the nest, possibly due to difficulty  
368 with body or nest temperature regulation, or increased recesses to obtain water as a result of



369 increased nest level air temperature and lower winds, could be more susceptible to depletion of  
370 stored resources during the incubation fast (Hanssen et al. 2002; Bottitta et al. 2003; Sénéchal et  
371 al. 2011). Further, greater nest movements may put females at a higher risk of attracting more  
372 attention from predators such as gulls, arctic foxes (*Vulpes lagopus*), and polar bears (Smith et al  
373 2012; Jagielski et al. 2021). In the case of high wind speeds where movements were shown to  
374 decrease, females may remain still to avoid detection from gulls taking advantage of windy  
375 conditions (Gilchrist and Gaston 1997; Gilchrist et al. 1998; Allard 2006). Furthermore,  
376 preliminary investigations at the East Bay Island colony suggest that the foraging success of  
377 polar bears is partially due to on-nest eider movements attracting bears to their nest locations  
378 (Geldart 2021). While we were unable to account for the effect of bear presence on eider  
379 incubation due to the lack of certainty in comprehensive island-wide video data, our research  
380 demonstrates that future studies on the connection between multiple stressors, incubation  
381 behaviour and predation risk, represents an important avenue for future investigation,  
382 particularly given the increasing predation pressures some seabirds are concurrently facing  
383 (Noyes et al. 2009; Smith et al. 2010; Kimberly and Salice 2013; Iverson et al. 2014; Prop et al.  
384 2015).

385         The interactive effect of temperature and THg levels on incubation behaviour  
386 demonstrated that at higher temperatures, individuals with greater THg levels had less  
387 movements than those with lower THg levels. Our prediction was that higher THg levels would  
388 result in greater movements due to reductions in PRL that may negatively impact incubation  
389 consistency (Tartu et al. 2015, 2016). However, in our study, the combination of THg and heat  
390 stressors resulted in less incubation interruptions, potentially due a more complex system than  
391 anticipated that includes the reaction of females to acute heat stress, as well as the supressing

392 effect of THg on CORT, which in-turn may interact with PRL levels (Provencher et al. 2016;  
393 Tartu et al. 2015; 2016; Choy et al. 2021). Females with lower THg levels may have a  
394 heightened acute stress response to heat exposure outside of their thermal limits, releasing CORT  
395 that supresses PRL and results in greater incubation interruptions (Tartu et al. 2015; 2016; Choy  
396 et al. 2021). While this action is a potential self-preservation method to obtain water and prevent  
397 dehydration, the female risks egg overheating and greater predation risk due to female absence  
398 and movements attracting predators (Smith et al 2012; Geldart 2021; Ridley et al. 2021).  
399 Meanwhile, females with higher THg levels may reduce this stress response, thus resulting in  
400 fewer incubation interruptions, but which have the potential to risk greater water loss and  
401 dehydration, thus higher mass loss that may be detrimental to female health (Parker and Holm  
402 1990; Ridley et al. 2021). However, these mechanistic linkages between THg, CORT and PRL  
403 have not been tested in relation to heat stressors and represents a complex system that is of future  
404 research interest due to the potential impacts on incubation duration, endogenous resource  
405 mobilization rates and dehydration, and predation risk (Olson et al. 2006; Hart et al. 2016;  
406 Høyvik Hilde et al. 2016). Additionally, THg and low CORT have been linked with weaker  
407 immune systems, higher oxidative stress, and greater lipid metabolism rates, which may  
408 cumulatively put female eider endogenous resource stores and overall health at greater risk  
409 (Fallacara et al. 2011; Whitney and Cristol 2017; Vagasi et al. 2018). Therefore, the deleterious  
410 effects of THg on the female's immune systems and metabolic rates, coupled with the reported  
411 positive effect of higher CORT on immune system response and reduced oxidative damage  
412 (Vagasi et al. 2018), may also be further complex, yet key factors that influence her incubation  
413 behaviour, especially in stressful thermal environments.

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

423

## 424 **5. Conclusion**

425 Arctic seabird colonies are being exposed to increasingly warming conditions and the effects of  
426 contaminants (Muir et al. 1999; Macdonald et al. 2000; Dietz et al. 2009; Mallory and Braune  
427 2012; Foster et al. 2019). We found that higher air temperatures, in combination with lower THg  
428 levels, correlated with laying phenology and decreased incubation interruptions in female  
429 common eiders. These results demonstrate that even sub-lethal THg levels (considered low) can  
430 have negative downstream consequences on incubation consistency when females are breeding  
431 under elevated air temperatures. These effects are expected to subsequently generate impacts on  
432 reproductive success and female health. Taken together, these combined results show it is  
433 important to examine the full suite of benefits and costs that climate change may generate for  
434 marine birds such as eiders at all stages of reproduction. Overall, interactive effects of multiple  
435 stressor exposure are an increasingly important research avenue due to the potential implications  
436 on reproductive success and, in the long-term, offspring recruitment and colony subsistence.

437

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775 **Tables and Figures**

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

780

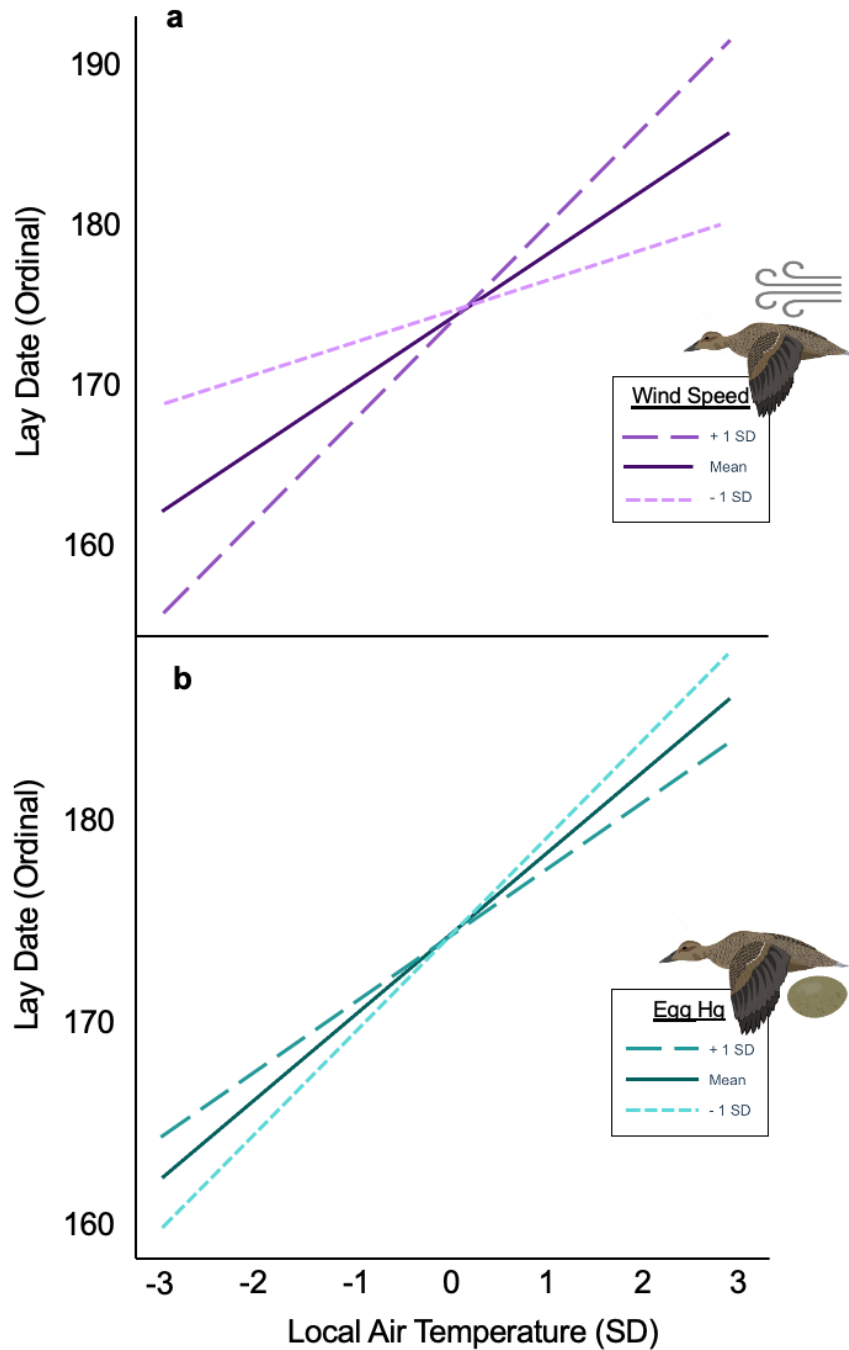
	<b>Mean</b>	<b>Standard Deviation</b>	<b>Range</b>
<b><i>2016</i></b>			
<b>Yolk</b>	0.06	0.02	0.04 - 0.11
<b>Albumen</b>	2.49	0.86	1.23 – 4.11
<b>Total Egg</b>	1.28	0.44	0.68 – 2.11
<b><i>2017</i></b>			
<b>Yolk</b>	0.08	0.02	0.05 – 0.12
<b>Albumen</b>	2.86	1.21	1.24 – 5.37
<b>Total Egg</b>	1.47	0.61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

781



782 **Table 2.** Results of two statistical models examining a) predictors of lay date (objective 1), and  
 783 (b) the number of incubation interruptions by individual weather exposure of common eider at  
 784 East Bay Island (Mitivik), Nunavut, Canada (objective 3), with random effects including the  
 785 number of incubation interruptions by incubation stage, hen ID (0-61), and section of the day  
 786 (0:00-5:59, 6:00-11:59, 12:00-17:59, 18:00-23:59). Objective (a) used data collected from 2016-  
 787 2019 (n=86), while objective (b) used data only from 2018 and 2019 (n=61). Significant p-values  
 788 are bolded.

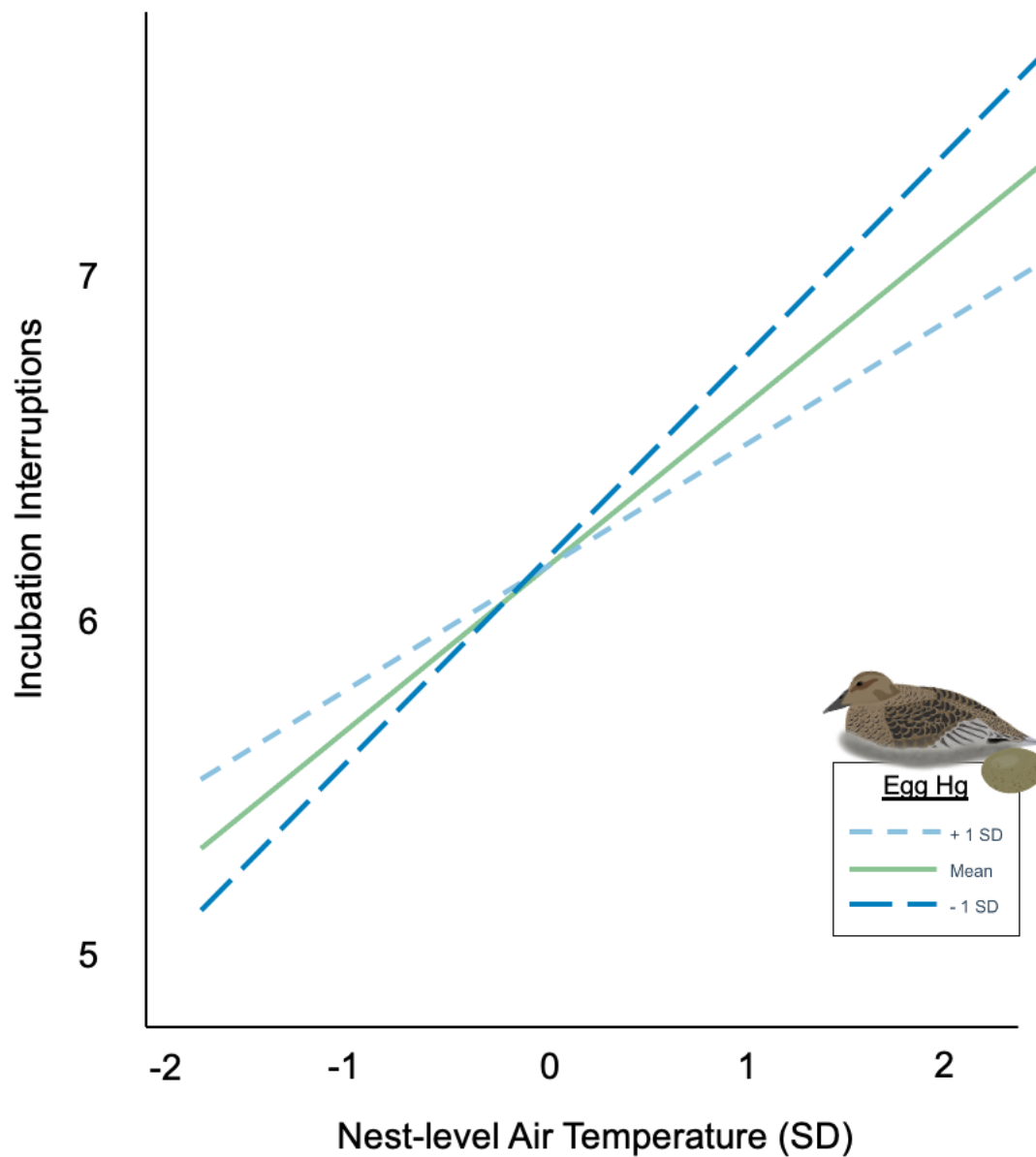
<i>(a) Lay Date – Generalized Linear Model</i>				
<b>Variable</b>	<b>Estimate (<math>\beta</math>)</b>	<b>SE</b>	<b>t</b>	<b>p-value</b>
Intercept	1935.231	782.138	2.474	<b>0.016</b>
Year	-0.873	0.388	-2.251	<b>0.027</b>
Temperature	4.039	0.441	9.152	<b>&lt;0.001</b>
Wind	-0.335	0.341	-0.984	0.328
THg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



789

790

791 **Figure 1.** Output from a GLM (Generalized Linear Model) with a normal distribution, showing  
 792 significant patterns between a) air temperature ( $^{\circ}\text{C}$ ) standard deviation (SD) and wind speed  
 793 (km/hr) (both measured over the five days prior to the rapid follicle growth (RFG) period) and b)  
 794 air temperature ( $^{\circ}\text{C}$ ) SD and egg THg levels ( $\mu\text{g/g}$  dry weight) in explaining variation in  
 795 common eider lay date (ordinal) from 2016-2019 at East Bay Island (Mitivik), Nunavut, Canada.



796  
 797 **Figure 2.** Output from a GLMM (Generalized Linear Mixed Model) with a normal distribution,  
 798 showing the interaction between nest-level air temperature ( $^{\circ}\text{C}$ ), and total first-laid egg Hg ( $\mu\text{g/g}$   
 799 dry weight) represented by standard deviations (SD) from the mean. Shown is the interaction  
 800 explaining variation in the number of on-nest movements a female common eider made over a 6-  
 801 hour period during incubation (data collected in July 2018 and 2019 from 61 eider nests located  
 802 at East Bay Island (Mitivik), Nunavut, Canada).

803 **Supplemental Materials**

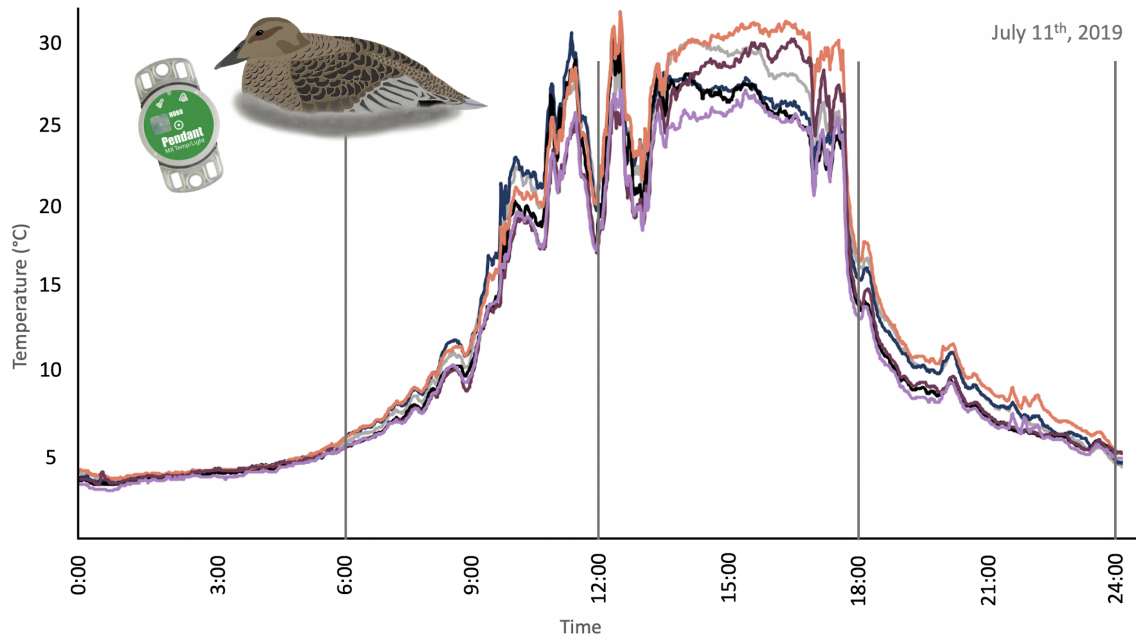
804 The mean air temperature and wind speed over the five days before the rapid follicle growth  
 805 (RFG) period for each year as determined from data collected from the Coral Harbour Weather  
 806 Station, mean lay dates, sample size of common eider nests at East Bay Island (Mitivik),  
 807 Nunavut, Canada in 2018 and 2019 through early (days 4-7), mid (days 12-15) and late  
 808 incubation (days 18-24), the mean incubation duration, as well as the mean number of eider  
 809 movements on the nest over a 24-hour period.

810

	<b>2016</b>	<b>2017</b>	<b>2018</b>	<b>2019</b>
<b>Mean Temperature (°C)</b>	5.18 ± 1.57	4.31 ± 2.43	3.19 ± 1.22	2.28 ± 0.52
<b>Mean Wind (km/hr)</b>	18.75 ± 5.90	24.31 ± 8.46	16.50 ± 3.81	19.78 ± 4.38
<b>Mean Lay Date</b>	June 28 ± 4.13	June 22 ± 4.12	June 26 ± 3.35	June 18 ± 3.33
<b>Early Incubation (n)</b>	-	-	26	23
<b>Mid Incubation (n)</b>	-	-	10	26
<b>Late Incubation (n)</b>	-	-	0	10
<b>Incubation Duration (days)</b>	-	-	10 ± 4 days	18 ± 5 days
<b># Movements</b>	-	-	26 ± 6	24 ± 5

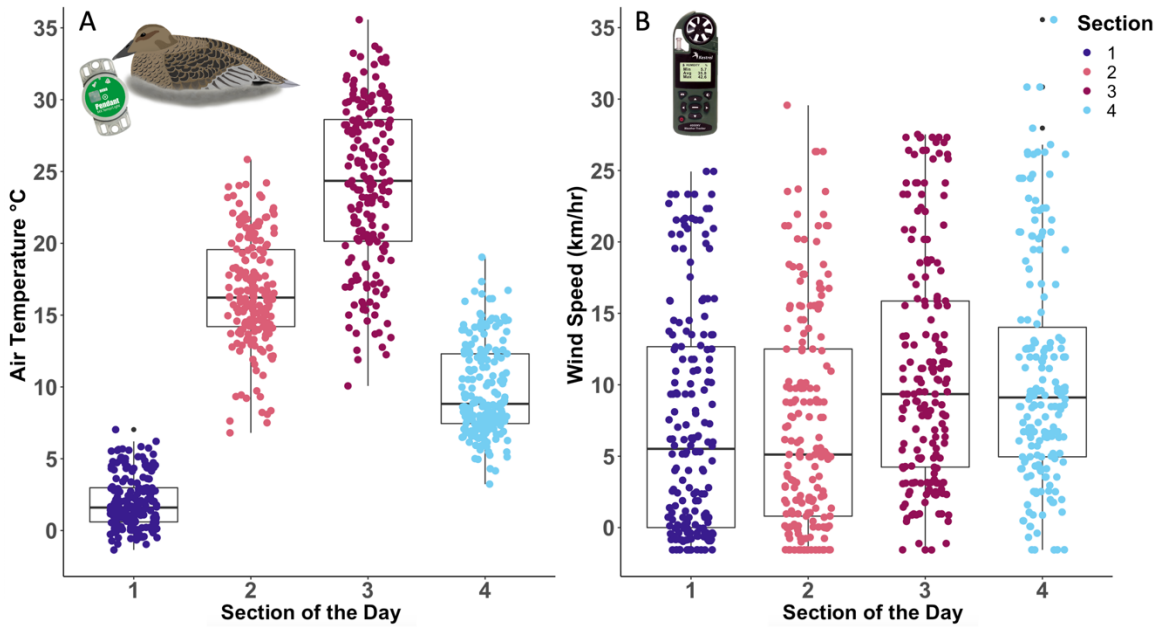
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813

814 Variation in air temperature throughout 24 hours at six common eider nests within the subset  
815 monitored for this study at East Bay Island (Mitivik), Nunavut, Canada on July 11<sup>th</sup>, 2019. Four  
816 sections of the day were examined, based on coldest (0:00-5:59), warming (6:00-11:59), hottest  
817 (12:00-17:59), and cooling (18:00-23:59) periods of the day.



818

819

820 Variations in air temperature (A) and wind speed (B) over 95 days at the nests of 61 incubating  
 821 common eiders monitored at Mitivik, Nunavut, Canada during July in 2018 and 2019. Air  
 822 temperature and wind speed were measured throughout the 24-hour period within four sections:  
 823 1 (0:00-5:59), 2 (6:00-11:59), 3 (12:00-17:59), and 4 (18:00-23:59). Horizontal lines within  
 824 boxes represent the median, and whiskers represent the standard error.