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Do foraging ecology and contaminants interactively predict parenting hormone levels in common eider?

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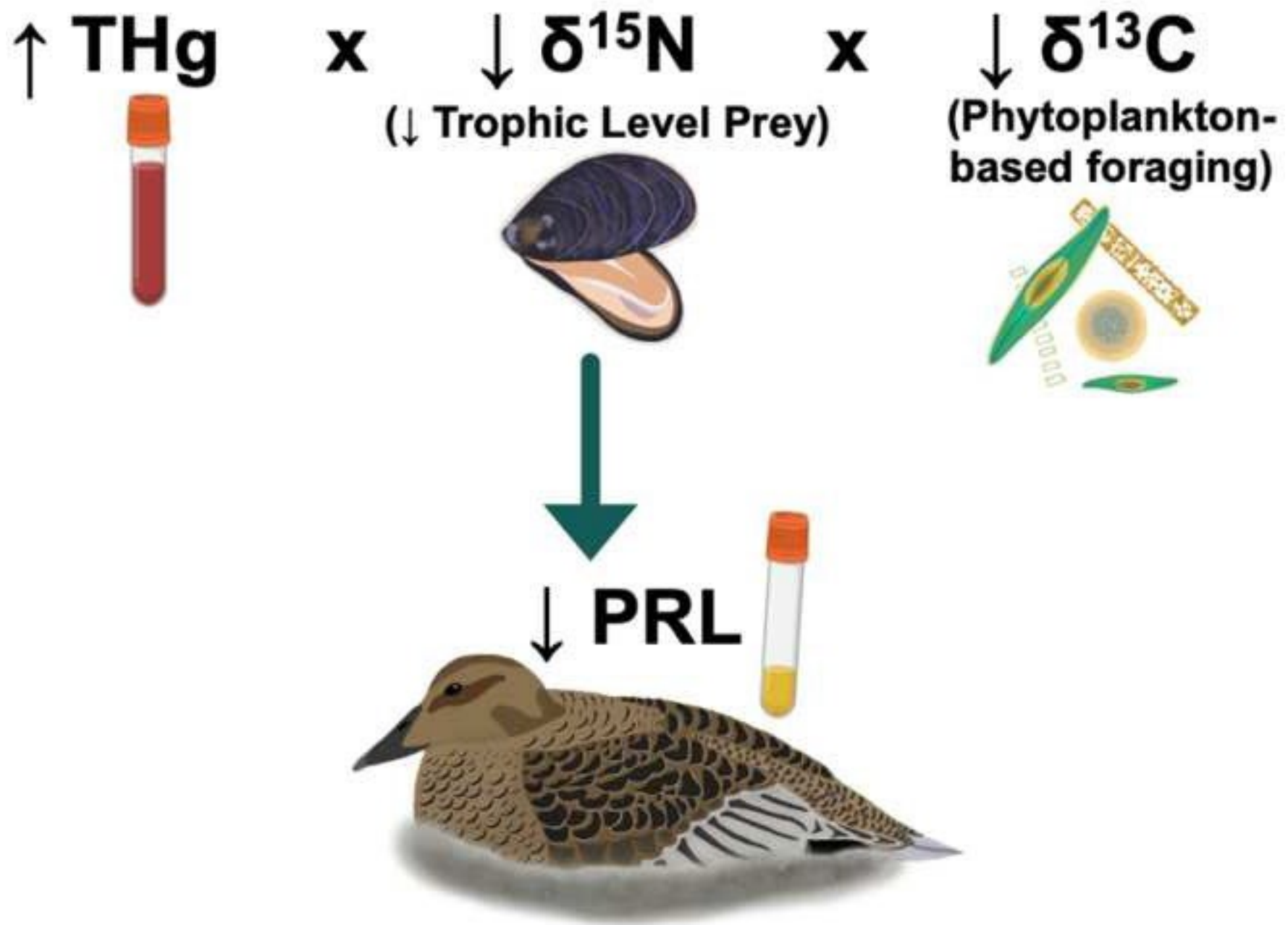
Abstract:

Global climate change is causing abiotic shifts such as higher air and ocean temperatures and disappearing sea ice in Arctic ecosystems. These changes influence Arctic-breeding seabird foraging ecology by altering prey availability and selection, affecting individual body condition, reproductive success, and exposure to contaminants such as mercury (Hg). The cumulative effects of alterations to foraging ecology and Hg exposure may alter the secretion of key reproductive hormones such as prolactin (PRL), important for parental attachment to eggs and offspring and overall reproductive success. However, more research is needed to investigate the relationships between these potential links. Using data collected from 106 incubating female common eiders (*Somateria mollissima*) at six Arctic and sub-Arctic colonies, we examined whether the relationship between individual foraging ecology (assessed using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and total Hg (THg) exposure predicted PRL levels. We found a significant, complex interaction between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg on PRL, suggesting that individuals cumulatively foraging at lower trophic levels, in phytoplankton-dominant environments, and with the highest THg levels had the most constant significant relationship PRL levels. Cumulatively, these three interactive variables resulted in lowered PRL. Overall, results demonstrate the potential downstream and cumulative implications of environmentally induced changes in foraging ecology, in combination with THg exposure, on hormones known to influence reproductive success in seabirds. These findings are notable in the context of continuing environmental and food web

changes in Arctic systems, which may make seabird populations more susceptible to ongoing stressors.

Highlights

- Blood samples from 106 common eiders from 6 colonies were analyzed ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, THg, prolactin)
- A significant interaction was found between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and Hg on prolactin
- In the 3-way interaction, $\delta^{15}\text{N}$ positively correlated with incubating prolactin
- Low $\delta^{13}\text{C}$ and high Hg had a consistent interactive impact in combination with $\delta^{15}\text{N}$
- This complex interaction may have downstream implications for reproductive success



1 **Do foraging ecology and contaminants interactively predict parenting hormone levels in**
2 **common eider?**

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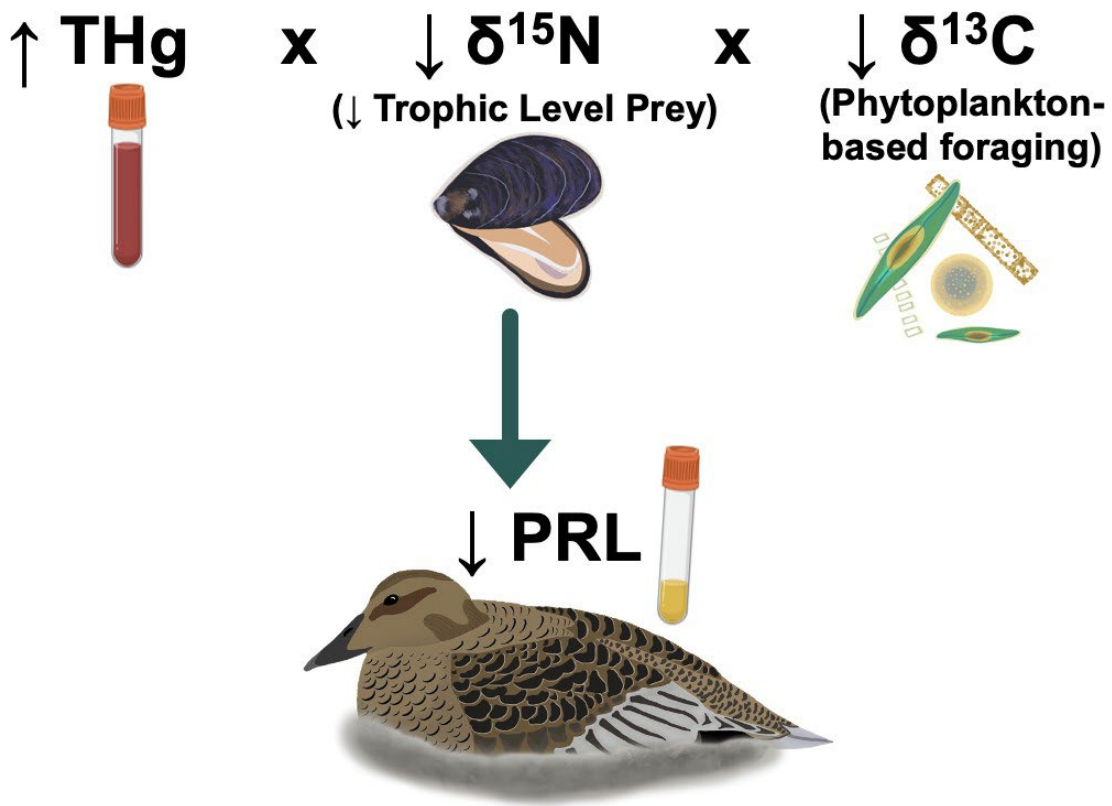
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36 THg, prolactin)
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41

42 **Graphical Abstract**



43

44 **Abstract**

45 Global climate change is causing abiotic shifts such as higher air and ocean temperatures and
46 disappearing sea ice in Arctic ecosystems. These changes influence Arctic-breeding seabird
47 foraging ecology by altering prey availability and selection, affecting individual body condition,
48 reproductive success, and exposure to contaminants such as mercury (Hg). The cumulative
49 effects of alterations to foraging ecology and Hg exposure may alter the secretion of key
50 reproductive hormones such as prolactin (PRL), important for parental attachment to eggs and
51 offspring and overall reproductive success. However, more research is needed to investigate the
52 relationships between these potential links. Using data collected from 106 incubating female
53 common eiders (*Somateria mollissima*) at six Arctic and sub-Arctic colonies, we examined
54 whether the relationship between individual foraging ecology (assessed using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and
55 total Hg (THg) exposure predicted PRL levels. We found a significant, complex interaction
56 between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and THg on PRL, suggesting that individuals cumulatively foraging at lower
57 trophic levels, in phytoplankton-dominant environments, and with the highest THg levels had the
58 most constant significant relationship PRL levels. Cumulatively, these three interactive variables
59 resulted in lowered PRL. Overall, results demonstrate the potential downstream and cumulative
60 implications of environmentally induced changes in foraging ecology, in combination with THg
61 exposure, on hormones known to influence reproductive success in seabirds. These findings are
62 notable in the context of continuing environmental and food web changes in Arctic systems,
63 which may make seabird populations more susceptible to ongoing stressors.

64 **1. Introduction**

65 Increasing anthropogenic activity has resulted in rapid and wide-ranging abiotic shifts in marine
66 systems associated with climate change, including rising air and ocean temperatures (Screen and
67 Simmonds 2010; Najafi et al. 2015), changes in ocean circulation and salinity (Timmermans et
68 al. 2011; Zika et al. 2018), and dramatic changes in sea ice abundance and distribution within
69 polar systems (Johannessen et al. 2004; Hoegh-Guldberg and Bruno 2010). Arctic regions
70 disproportionately exhibit these simultaneous, cumulative effects (IPCC 2019; AMAP 2021),
71 resulting in impacts on food web relationships (Vasseur and McCann 2005; Frederiksen et al.
72 2006; Parmesan 2006; Pecuchet et al. 2020). Alterations in the abundance and distribution of
73 lower trophic level organisms (i.e., primary producers) have been evident, with organisms such
74 as phytoplankton displaying advanced phenology and higher abundance relative to sea ice algae
75 (Frederiksen et al. 2006; Renaut et al. 2018; Lewis et al. 2020). Additionally, changes in higher
76 trophic level foraging ecology have been associated with climate change, as prey disruptions
77 further disturb the relationships among food webs (Moline et al. 2008; Watt et al. 2016). Thus,
78 bottom-up and top-down trophic level alterations can result in modifications to individual and
79 species foraging ecology and, in some cases, sizeable population declines (Legagneux et al.
80 2012; Perkins et al. 2018; Durant et al. 2019). Seabirds are particularly susceptible to adverse
81 outcomes resulting from changes in both directions of trophic alterations, which can influence
82 body condition and, importantly, downstream reproductive success (Baird 1990; Hamer et al.
83 1993; Suryan et al. 2006; Perkins et al. 2018; Hovinen et al. 2019). Additionally, changing
84 predator-prey dynamics and spatio-temporal prey abundance can alter, either positively or
85 negatively, individual seabird exposure to environmental contaminants such as mercury (Hg)

86 through changes in prey selection and foraging locale (Bearhop et al. 2000; Braune et al. 2014;
87 Fort et al. 2016, Tartu et al. 2022).

88 Arctic marine systems are contaminated with Hg via northward transportation of Hg
89 through air and ocean circulation as well as through Arctic rivers (Macdonald et al. 2000; Sonke
90 et al. 2018; DiMento et al. 2019), and the melting of the cryosphere which releases stored Hg
91 from years of higher contaminant output back into the system (Rydberg et al. 2010; Schuster et
92 al. 2018; Hawkings et al. 2021). These factors have all cumulatively resulted in spatiotemporally
93 heterogeneous environmental Hg levels in Arctic regions that influence organism Hg levels by
94 factors including spatio-temporal location and foraging ecology (Braune et al. 2005; 2015; Leu et
95 al. 2011; de la Vega et al. 2019; Albert et al. 2021(b)). Individuals foraging at higher trophic
96 levels, usually determined using nitrogen stable isotope analysis ($\delta^{15}\text{N}$, in relation to ^{15}N to ^{14}N
97 ratios), are often correlated with elevated Hg levels resulting from the methylmercury (MeHg)
98 biomagnification process, although individual variation outside of this correlation often exists
99 (Atwell et al. 1998; Bearhop et al. 2000; DiMento et al. 2019). Moreover, the influence of Arctic
100 marine primary producers on the diets of higher order predators, often determined using ratios of
101 carbon isotopes (^{12}C - phytoplankton enriched, ^{13}C - ice algae enriched; $\delta^{13}\text{C}$), can offer insight
102 into potential Hg sources based on foraging location and sea ice abundance (Hobson and Welch
103 1992; Hobson et al. 1995; McMahon et al. 2006).

104 MeHg is a biologically converted form of Hg that affects endocrine functioning,
105 behaviour, and reproductive success in birds at even low, sub-lethal levels (Wiener et al. 2003;
106 Whitney and Cristol 2017; Evers 2018, Chastel et al. 2022). While the Hg levels in most seabirds
107 (95%) are considered lower risk, there have been recent calls to examine the potential impact of
108 Hg in a cumulative stressor framework to help address Article 22 of the Minimata Convention

109 (https://www.mercuryconvention.org/sites/default/files/documents/information_document/4_INF
110 [12_MonitoringGuidance.English.pdf](#)). Article 22 calls for an evaluation of the effectiveness of
111 the convention, in which Arctic seabirds serve as indicators for assessing environmental
112 contamination (Chastel et al. 2022). Avian reproduction can be affected by Hg exposure through
113 its endocrine-disrupting properties that can influence female breeding behaviour (Tan et al. 2009;
114 Ackerman et al. 2016; Whitney and Cristol 2017, Chastel et al. 2022). For example, in the
115 beginning stages of reproduction, sub-lethal Hg has been correlated with a decreased likelihood
116 to breed, attributed to the effect of Hg on luteinizing hormone (LH) and the subsequent release of
117 sex hormones (i.e., estrogen; Tartu et al. 2013; 2014). Importantly, exposure to Hg has been
118 linked to a decrease in prolactin (PRL), a pituitary hormone key for parental care behaviours (El
119 Halawani et al. 1984; Tartu et al. 2015; Angelier et al. 2016; Tartu et al. 2016). However, no link
120 between Hg and PRL has been observed in other studies, indicating a potentially complex
121 relationship and role of PRL in avian incubation (Gilmour et al. 2019; Blévin et al. 2020).

122 In birds, PRL secretion commences after the parent physically touches their eggs and
123 increases following the cessation of laying and the onset of incubation behaviour (Buntin 1996;
124 Sockman et al. 2000). In common eider (*Somateria mollissima*, hereafter eider), PRL increases at
125 the onset of incubation and remains at a consistent level during incubation, followed by a steep
126 increase immediately before hatching (Criscuolo et al. 2002). Additionally, the role of PRL in
127 clutch size determination has been previously proposed, with increased PRL signalling for a
128 decrease in LH that stops the laying period in anticipation of incubation (Sockman et al. 2000).
129 Disruption of PRL secretion during incubation has been proposed as a likely mechanistic link
130 that results in lowered quality of incubation behaviour via decreased incubation attentiveness
131 (Angelier and Chastel 2009; Angelier et al. 2009). Incubating females in worsened body

132 condition may have lower PRL levels, thus reducing incubation quality and increasing predation
133 risk (Criscuolo et al. 2002). Overall, the cumulative and interactive effects of prey consumption
134 and Hg accumulation on PRL can influence key reproductive traits such as incubation behaviour
135 and reproductive success. These linkages are important to examine, especially given the
136 accelerating rate of environmental shifts in Arctic marine systems.

137 A recent study from our group indicated that eider colonies highly varied in
138 multidimensional niche dynamics: migratory colonies had higher $\delta^{15}\text{N}$ and THg, but lower $\delta^{13}\text{C}$
139 and sea-ice cover positively correlated with $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg (Smith et al. 2021). The study
140 also found that individual eiders with lower $\delta^{13}\text{C}$ and higher trophic positions had higher THg
141 (Smith et al. 2021). In the current study, we built from these results to examine the interactive
142 effects of foraging ecology, inferred with stable isotope analysis (Kelly 2000), and Hg on PRL
143 levels of incubating female common eiders. Eiders are long-lived, colonial-nesting marine ducks
144 with dispersed breeding populations across the circumpolar and sub-Arctic. As such, they are
145 exposed to diverse environmental conditions, which influence variation in their foraging ecology
146 and Hg exposure (Albert et al. 2021(a); Smith et al. 2021). Eider prey includes a diversity of
147 benthic invertebrates (e.g., urchins and mussels) and pelagic macroinvertebrates (e.g.,
148 amphipods; Sénéchal et al. 2011). Eiders forage extensively in the pre-breeding period in various
149 ice conditions depending on the timing of spring melt to obtain an appropriate body condition
150 needed to breed (Jean-Gagnon et al. 2018). Importantly, female eiders undergo a 24-26 day
151 uniparental incubation fast, relying solely on their endogenous stores to fuel the incubation
152 period (Hanssen et al. 2002; Bottitta et al. 2003; Sénéchal et al. 2011). During this fasting period,
153 contaminants including Hg increase in the blood due to the mobilization of endogenous lipid and
154 protein stores (Wayland et al. 2005; Bustnes et al. 2010; McPartland et al. 2020). These levels

155 can go over the threshold known to be negatively correlated with PRL secretion in other seabird
156 species (Tartu et al. 2015; 2016). Consequently, in combination with reduced body condition,
157 elevated blood levels of Hg may interfere with hormones such as PRL, with the potential for
158 downstream influences on incubation behaviour and reproductive success (Tartu et al. 2016).
159 However, intricate relationships between these and other physiological aspects have been
160 demonstrated previously in the literature. In common eiders, complex and integrated
161 relationships have been shown between clutch size, body condition/mass, incubation duration,
162 PRL and the primary glucocorticoid in birds, corticosterone (CORT) (Erikstad et al. 1993;
163 Criscuolo et al. 2006). Clutch size and body condition are positively related, while body
164 condition can be negatively correlated with incubation duration but positively correlated with
165 incubation attentiveness (Erikstad et al. 1993; Erikstad and Tveraa 1995). Meanwhile, body mass
166 was positively linked to PRL levels, while baseline levels of CORT were negatively correlated
167 with plasma PRL, altogether leading to reductions in overall reproductive success (Criscuolo et
168 al. 2002; 2005; 2006). These relationships provide a background for examining the effects of
169 foraging ecology and Hg on PRL in female eiders.

170 Our overall hypothesis was that the combined effects of foraging ecology and Hg
171 contamination would affect PRL levels in incubating eiders. Specifically, we predicted that lower
172 levels of PRL would be correlated with lower $\delta^{15}\text{N}$ (lower trophic level foraging, lesser quality
173 prey), higher $\delta^{13}\text{C}$ (sea ice algae-based foraging, more restrictive foraging environment), and
174 elevated Hg levels. Examining these relationships will allow for a more extensive determination
175 of the indirect mechanisms by which climate change affects at-risk Arctic seabird populations.

176

177 **2. Methods**

178 **2.1. Sample collection and physiological analysis**

179 Seven Arctic and sub-Arctic breeding colonies were monitored in 2018 (Table 2, N=136).
180 Incubating eiders were captured on their nests using noose poles, bownets, or dogs (John's Island
181 location only; Milton et al. 2016). A 200-1,000 μ L blood sample was collected from each
182 female's tarsal vein, jugular vein (Grindøya and Kongsfjorden), or brachial vein (Iceland) using
183 a 23G thin-wall, 1-inch needle attached to a heparinized 1 mL syringe (10 mL syringe -
184 Grindøya and Kongsfjorden). Samples were centrifuged within 8-12 h of collection at
185 approximately 10,000 rpm for 10 min to obtain red blood cells (RBC) for stable isotope (isotope-
186 ratio mass-spectrometer) and total Hg (THg; Advanced Mercury Analyser; see Smith et al. 2021
187 for further details on these methods and results). Plasma was collected from the centrifuged
188 whole blood, frozen for storage in the field, and later sent for PRL analysis to the Centre
189 d'Etudes Biologiques de Chizé (CEBC), France. Plasma samples were analyzed for PRL using
190 radioimmunoassay (RIA) following the procedure detailed in Cherel et al. (1994) and validated
191 in common eiders in previous studies (Criscuolo et al. 2002). The analysis consisted of
192 duplicates with colonies split into two runs: John's Island, Iceland and Tern Island in one run
193 (intra-assay variation = 12.01%), and Grindøya, Faroe Islands, Kongsfjorden, and Solovetskiy
194 Islands in a second run (intra-assay variation = 9.28%). Inter-assay variation between the two
195 runs was 14.75%, calculated from a sample run in both assays in 6 replicates. PRL was measured
196 in 10 μ L, and the lowest detectable limit was 0.45 ng/mL.

197 As specific individual incubation stage was unable to be determined at many sites or
198 hens, we could not correct the potential effect of incubation fasting on THg or $\delta^{15}\text{N}$ levels
199 (Hobson et al. 1993; Wayland et al. 2005; Smith et al. 2021). However, using RBCs to determine
200 isotopic and THg values minimized this effect as $\delta^{15}\text{N}$ enrichment is lesser in blood cells than in

201 plasma (Cherel et al. 2005). Further, as PRL levels are consistent throughout incubation stages in
202 eiders prior to hatching (Criscuolo et al. 2002), we were able to conduct inter-colony and
203 individual comparisons of PRL without correction for individual or colony incubation stage.
204

205 **2.2. Statistical analysis**

206 To examine whether PRL levels varied between colonies, we first ran an ANOVA followed by a
207 posthoc Tukey's Honest Significant Difference (HSD) test using the R package car v.3.0-10 (Fox
208 and Weisberg 2019). We then used compact letter display, in combination with the R package
209 ggplot2 v.3.3.6, to visually determine significance at an alpha level of 0.05 between the seven
210 colonies using the R package multcompView v.0.1-8 (Graves et al. 2015; Wickham 2016).

211 Following this, we calculated AICc values for 12 potential models to determine the most
212 parsimonious model using the R package AICcmodavg v.2.3-1 (Mazerolle 2020). The model
213 with the lowest AICc also had a significantly lower log-likelihood value, thus, was a better fit
214 than the other models (Table 1). We then used a general linear mixed model (GLMM) with a
215 normal distribution to determine the interactive effect of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg levels on PRL
216 secretion. The dependent variable was PRL, with $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg values included as fixed
217 independent variables in all single, two- and three-way interactions. Additionally, we included
218 female body mass (g) and clutch size as fixed independent variables in a two-way interaction. All
219 independent variables were standardized and centred for comparison to remove
220 misrepresentation of effects and increase the interpretability of coefficients (Schielezeth 2010).
221 We included breeding colony in the model as a random variable to control for inter-colony PRL
222 variation, with the objective being to examine individual variation. All statistical analyses were
223 conducted in RStudio version 2022.07.2 (RStudio Team). All model assumptions were met by

224 visually inspecting histograms to confirm a normal data distribution, quantile-quantile plots, and
225 residual plots from the model outputs. We also confirmed the absence of multicollinearity
226 between all variables using correlation coefficients and variance inflation factors (VIF), which
227 were below 0.36 and 3.90 (3-way interaction), respectively. In interpretations of three-way
228 interactions, the interaction among two factors (A * B) differs along with levels of a third factor
229 (C). To assist with the visualization of these complex relationships, significant interactions were
230 graphed using the R package Interactions v.1.1.3 (Long 2019). This package calculated Johnson-
231 Neyman intervals and simple slopes analysis to determine the significant slopes within the three-
232 way interaction.

233

234 **3. Results**

235 Median PRL levels were variable among eider colonies, ranging from 245.18 ng/mL (Tern
236 Island) to 348.99 ng/mL (Kongsfjorden), with the median PRL for all eiders at 287.60 ng/mL
237 (Table 2, Figure 2). At the individual eider level, the lowest (142.72 ng/mL) and highest (489.20
238 ng/mL) values were found at the Kongsfjorden colony. Mean colony PRL levels significantly
239 varied between colonies, with the Kongsfjorden colony having significantly higher mean PRL
240 levels than every colony except for Grindøya (Figure 2). Conversely, Tern Island had
241 significantly lower mean PRL levels than all colonies but Faroe Islands (Figure 2). Although we
242 report the PRL values for the John's Island colony, researchers at this location did not collect
243 body mass measurements. Therefore, this colony was omitted from the statistical model ($n=18$)
244 and any individuals that did not have body mass and/or clutch size data ($n=12$, total individuals
245 omitted = 30), with a remaining sample size of 106 individuals for the GLMM.

246 The GLMM showed that $\delta^{15}\text{N}$ ($t_{80}=2.289$, $p=0.025$; Table 3) as well as the three-way
247 interaction between $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg were significant ($t_{95}=2.089$, $p=0.039$; Table 3). Johnson-
248 Neyman intervals and simple slopes analysis determined that 6/9 of the slopes in the three-way
249 interaction were significantly different from zero. In particular, 3/3 slopes were significant at
250 THg +1 standard deviation (SD), 2/3 were significant at mean THg levels, and 1/3 were
251 significant THg -1 SD (Figure 3). At higher levels of THg (+1 SD), all levels of $\delta^{13}\text{C}$ values (-1
252 SD, mean, and +1 SD) resulted in significant positive relationships between $\delta^{15}\text{N}$ and PRL
253 (Figure 3). At mean THg levels, mean and low $\delta^{13}\text{C}$ values (-1 SD) also resulted in significant
254 positive relationships between $\delta^{15}\text{N}$ and PRL (Figure 3). At low THg levels (-1 SD), only low
255 $\delta^{13}\text{C}$ values (-1 SD) resulted in significant positive relationship between $\delta^{15}\text{N}$ and PRL (Figure
256 3). However, there was no significant relationship between female body mass, clutch size, or a
257 two-way interaction of those variables with PRL (Table 3).

258

259 **4. Discussion**

260 We examined the interactive effects of individual foraging ecology and THg contamination on
261 PRL levels in incubating female common eiders across six colonies at a pan-Arctic scale. We
262 predicted an effect of the interaction between $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg on PRL levels, given the
263 potential effect of these variables on female body condition and hormone regulation. Consistent
264 with our prediction, individuals at lower trophic levels (lower $\delta^{15}\text{N}$) showed the lowest PRL
265 levels, most commonly in combination with individuals at higher THg levels and those foraging
266 in predominantly phytoplankton-based environments (lower $\delta^{13}\text{C}$). Our findings suggest a
267 potential cumulative, interactive effect of foraging ecology and elevated THg exposure on PRL
268 levels in wild eider colonies.

269

270 ***4.1. Interactive relationship between foraging ecology and PRL levels***

271 We found a significant positive relationship between $\delta^{15}\text{N}$ and PRL levels. Pre-breeding eiders
272 foraging at lower trophic levels may potentially have a relatively lower body condition going
273 into and then throughout incubation. PRL and incubating body condition have been linked in
274 previous studies, where lower-condition females showed reduced PRL levels (Criscuolo et al.
275 2002). Although body mass did not correlate with PRL, there is nonetheless potential for the
276 indirect linkages between trophic level (i.e., $\delta^{15}\text{N}$) and body condition to influence PRL secretion
277 (see section 4.3). Changes in food web structure are apparent with continuing climate change and
278 are likely to vary spatio-temporally between colonies with differing prey availability (see section
279 1; Smith et al. 2021). These effects are important for a species such as eiders since a lower body
280 condition beginning in the pre-breeding stage could reduce the amount of PRL during
281 incubation, with potential implications on nest attentiveness and overall breeding success
282 (Erikstad et al. 1993; Criscuolo et al. 2002). Eiders forage primarily on amphipods and bivalves,
283 which have demonstrated sensitivity to warming ocean temperatures (Węśławski et al. 2011;
284 Dalpadado et al. 2016; Vinarski et al. 2021). Based on our current results, changes in eider
285 trophic niches due to ecosystem shifts (likely to vary widely and depend on spatio-temporal prey
286 availability) may have downstream impacts on body condition and PRL levels. For example,
287 individuals that consume a greater abundance of lower trophic level prey could have
288 comparatively lower body condition with expected negative impacts on PRL levels. This prey
289 may include bivalves, which have lower energy returns due to a low ratio of flesh content to shell
290 size compared to shell-less macroinvertebrates (Hamilton et al. 1999; Schummer et al. 2008). In
291 colonies where trophic niches shift to a greater abundance of higher trophic level prey, such as

292 arthropods, the reverse effect is possible where higher trophic level prey may improve
293 reproductive output, as seen in blue-footed boobies (González-Medina et al. 2018). Interestingly,
294 the colonies with the lowest median PRL levels (Faroe Islands, Tern Island) were also identified
295 previously as having the lowest median $\delta^{15}\text{N}$ out of the colonies studied (Smith et al. 2021),
296 indicating that their lower PRL values may be linked with their utilization of lower trophic level
297 prey such as bivalves. Despite these potential patterns, the eventual outcome of prey abundance
298 shifts on eider hormonal mechanisms at the heart of successful incubation outcomes remains to
299 be seen as climate change effects increase annually. However, our work provides a valuable
300 baseline to examine subsequent future changes.

301 We also detected a significant relationship between $\delta^{13}\text{C}$ and PRL levels in combination
302 with $\delta^{15}\text{N}$ and THg. Along with the food web changes described with $\delta^{15}\text{N}$ above, the most
303 consistently detected relationship was associated with phytoplankton-based foraging (low $\delta^{13}\text{C}$)
304 and PRL levels in our three-way interaction. Due to the increasing effects of climate change,
305 phytoplankton blooms are expected to become more intense and occur earlier in the year (Kahru
306 et al. 2011; Ardyna and Arrigo 2020). Phytoplankton blooms are also increasingly apparent
307 when sea ice is still present, even in the benthos, due to increased light transmission with
308 thinning ice (Arrigo et al. 2012; Horvat et al. 2017; Shiozaki et al. 2022). In eiders,
309 phytoplankton blooms in the Baltic Sea have been linked to a reduction in nesting eiders
310 (Larsson et al. 2014). In this study, the relationship was suggested to be connected to an impact
311 of the phytoplankton bloom on blue mussel (*Mytilus edulis*) availability (either through toxic or
312 non-toxic pathways), followed by a subsequent reduction in eider body condition that impacted
313 their breeding propensity (Larsson et al. 2014). Our results showing a consistently significant
314 effect of low $\delta^{13}\text{C}$ in our three-way model on PRL may be related to phytoplankton-based

315 environments resulting in less prey availability (such as blue mussels), either quality or quantity,
316 that affects eider body condition and subsequently PRL.

317 Conversely, we also detected a significant relationship between sea ice algae-based
318 foraging (high $\delta^{13}\text{C}$) and PRL levels in our three-way interaction, only in high THg individuals.
319 The relationship between high $\delta^{13}\text{C}$ and PRL, along with elevated THg, may be due to
320 constraints in foraging areas with higher sea ice cover, as seen previously in eiders that rely on
321 access to open water to reach benthic and pelagic areas (Jean-Gagnon et al. 2018). As such,
322 constraints in prey availability, combined with a high proportion of ice cover, could result in
323 lower energetic stores (i.e., body condition) available to eiders during incubation, with possible
324 downstream impacts on PRL levels.

325 Overall, the relationships we have detected between foraging ecology (based on isotopic
326 niche) and PRL provide an initial look into how pre-breeding prey selection may indirectly
327 influence key reproductive hormones in eiders. Future studies may benefit from integrating
328 research into whether pre-breeding prey availability and quality may influence incubating PRL.

329

330 ***4.2. Importance of THg levels in relation to incubating PRL***

331 The interactive relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with PRL, as described in section 4.1, was
332 most often significant in combination with high THg. The importance of THg in this relationship
333 could potentially relate to the endocrine-disrupting properties of THg (Zhu et al. 2000; Tan et al.
334 2009). In addition, negative relationships between THg and body condition, as seen in previous
335 studies (Provencher et al. 2016; but see Carravieri et al. 2022), may have also played a role in the
336 effect of THg on PRL in combination with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Importantly, our findings support
337 concern over THg as an important component of cumulative stressors systems in the Arctic,

338 where the combination of stressors such as contaminants, climate change and food web dynamics
339 are expected to have cumulative impacts on birds (Chastel et al. 2022; Esparza et al. 2022; Smith
340 et al. 2022). Overall, we found that THg played an important interactive role along with foraging
341 ecology on PRL levels. However, whether this is related to the direct effects of THg on PRL, or
342 indirectly mediated by foraging ecology or other intermediate physiological parameters is
343 unclear and requires further study.

344

345 ***4.3. Other physiological and external factors with a potential influence on PRL***

346 We were able to examine the relationship between body mass and PRL levels in this study.
347 However, while previous studies successfully used this metric to determine eider body condition
348 (Descamps et al. 2011), this measure of female condition may have been an incomplete look into
349 the relationship between body condition and PRL in incubating eiders. Body condition, often
350 measured as body mass divided by total head length (Jamieson et al. 2006) or scaled mass index
351 (Peig and Green 2009), may provide a more in-depth look into female quality at the time of
352 sampling, rather than only body mass which does not adjust for overall body size. Additionally,
353 individual body mass declines as eiders progressively use their endogenous resources during
354 their incubation fast (Criscuolo et al. 2002; Hanssen et al. 2002). We were unable to control the
355 incubation stage or body size in this study, but this would be ideal for future research on this
356 topic.

357 It is worth highlighting that the primary glucocorticoid hormone in birds, corticosterone
358 (CORT), is an important factor in eider pre-incubation body condition, where higher baseline
359 CORT corresponds to more intensive foraging in eiders (Hennin et al. 2015; 2018). Baseline
360 CORT may play an essential regulating role in the relationship we have detected between PRL

361 and foraging ecology during pre-breeding periods. For example, during pre-breeding foraging,
362 females with higher baseline CORT may result in downstream elevated PRL levels during
363 incubation due to more intensive foraging, leading to higher body conditions at the start of
364 incubation (Criscuolo et al. 2002; Angelier et al. 2016). Additionally, elevated baseline CORT
365 has also been linked to a greater need for resources during incubation, as seen in incubating
366 macaroni penguins (*Eudyptes chrysolophus*; Crossin et al. 2012). Eiders, which fast during one
367 single incubation bout, have demonstrated a negative relationship between CORT and PRL
368 during incubation periods in previous studies that regulates incubation behaviour (Criscuolo et
369 al. 2005; 2006). The same pattern has been seen in birds that forage during incubation, with
370 stressed individuals leaving more often on foraging trips (Angelier and Chastel 2009; Angelier et
371 al. 2009). In addition, elevated CORT levels may negatively affect female immunity and mass
372 loss during incubation, as seen in previous common eider studies (Bourgeon and Raclot 2006;
373 Bourgeon et al. 2009). Higher energetic stress could have foraging ecology-mediated links to
374 PRL levels. While high CORT levels may be initially beneficial during the pre-breeding period,
375 these elevated may be detrimental to PRL during incubation, especially in fasting female eiders.
376 Further implications may also arise from the added effects of elevated stress-induced CORT,
377 especially as predator-prey relationships and climate conditions shift in Arctic systems.

378 Many eider colonies are facing increasing predation pressure from polar bears (*Ursus*
379 *maritimus*), arctic foxes (*Vulpes lagopus*) and *Larus* sp. gulls (Smith et al. 2012; Hanssen et al.
380 2013; Prop et al. 2015; Jagielski et al. 2021). Eiders must also contend with elevated thermal
381 environments that can influence female incubation behaviour, especially when combined with
382 Hg exposure (Smith et al. 2022). Interestingly, studies on eiders in the Baltic Sea have
383 determined that those with elevated PRL and higher body condition may have higher nest

384 predation risk (Mohring et al. 2021). However, the correlation between PRL and elevated
385 predation risk was speculated to be attributed to an absence of low-quality individuals with
386 reduced PRL levels at nesting sites with higher predation risk (Mohring et al. 2021). In general,
387 lower PRL may result in a greater risk for egg predation due to lowered incubation consistency.
388 In comparison, higher PRL, thus greater incubation consistency, may lead to higher female
389 predation risk. However, further research is needed to establish these links. Ultimately, the
390 cumulative stressors eiders are now more often exposed to both pre-breeding and during
391 incubation have the potential to greatly decrease nesting success with a ‘perfect storm’ of
392 stressors influencing reproductive parameters via PRL secretion. In this study, we were unable to
393 examine the links between PRL levels and eider breeding behaviour, predation, or nest success.
394 However, examining these metrics, along with foraging ecology and contaminant loads, would
395 provide holistic context to the implications of these stressors on avian reproductive success.

396

397 **Conclusion**

398 The interactive effects of foraging ecology and THg exposure on PRL levels were examined in
399 incubating female common eiders. Our results show that individuals with high THg that were
400 interactively foraging at lower trophic levels (low $\delta^{15}\text{N}$) and in areas with greater phytoplankton
401 abundance (low $\delta^{13}\text{C}$) had the most significant relationships resulting in lowered PRL levels.
402 Overall, this complex interactive system, based on foraging ecology and Hg exposure, may have
403 downstream implications for reproductive success through hormone alteration and, therefore,
404 population demography. These effects may be strengthened within the context of continually
405 changing environmental conditions on a global scale. However, further studies are required to

406 fully understand these complex relationships and their reproductive and demographic
407 consequences in a changing Arctic.

408

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784 **Tables and Figures**

785 **Table 1.** Results of model selection on plasma PRL levels of 106 female common eiders from 6
 786 breeding colonies. The number of parameters (k), corrected Akaike information criterion (AICc),
 787 change in AICc (Δ AICc), AICc weight, and log-likelihood are provided for each competing
 788 model. Colony was included as a random variable in all models, however, when clutch size was
 789 included as a random variable it is denoted with ^R.

Model	k	AICc	Δ AICc	AICc Weight	Log-likelihood
THg*δ^{15}N*δ^{13}C+Mass*Clutch	13	1106.61	0.00	0.80	-538.33
THg* δ^{15} N* δ^{13} C+Mass+Clutch	12	1109.70	3.09	0.17	-541.17
THg* δ^{15} N+THg* δ^{13} C+ δ^{15} N* δ^{13} C +Mass*Clutch	12	1113.91	7.30	0.02	-543.28
THg* δ^{15} N* δ^{13} C+Mass+Clutch ^R	12	1115.73	9.12	0.01	-544.19
THg* δ^{13} C+ δ^{15} N+Mass+Clutch	9	1123.24	16.63	0.00	-551.68
δ^{13} C* δ^{15} N+Mass+Clutch	8	1126.41	19.80	0.00	-554.46
THg+ δ^{15} N+ δ^{13} C+Mass+Clutch	8	1126.57	19.96	0.00	-554.54
δ^{15} N+Mass+Clutch	6	1136.47	29.86	0.00	-561.81
δ^{13} C+Mass+Clutch	6	1139.02	32.40	0.00	-563.08
THg+Mass+Clutch	6	1139.53	32.91	0.00	-563.34
THg* δ^{15} N* δ^{13} C+Mass	11	1173.26	66.64	0.00	-574.30
THg* δ^{15} N* δ^{13} C+Clutch	11	1191.18	84.57	0.00	-583.28
THg* δ^{15} N* δ^{13} C	10	1457.05	350.44	0.00	-717.64

790

791 **Table 2.** Locations of common eider colonies used in this study, sample size, month samples
 792 were obtained, colony coordinates as well as median and range of PRL levels.

Location	n	Sampling month	Latitude	Longitude	Female mass (g)	Median PRL (ng/mL)
Breiðafjörður, Iceland	21	June	65.078	-22.736	1780 ± 111.6	310.21 ± 57.02
Grindøya, Norway	17	June	69.633	18.844	2050 ± 168.3	336.50 ± 48.13
John's Island, Canada	18	July	43.645	-66.041	N/A	277.68 ± 49.58
Kirkjubøhólmur, Faroe Islands	16	July	61.950	-6.799	1400 ± 223.9	264.75 ± 41.13
Kongsfjorden, Norway	16	June	78.918	11.910	1525 ± 210.7	348.99 ± 82.29
Solovetskiy Islands, Russia	24	June	65.048	35.774	1800 ± 105.4	280.04 ± 49.38
Tern Island, Canada	24	June	69.547	-80.812	1660 ± 213.7	245.18 ± 44.65

793

794 **Table 3.** Results of a general linear mixed effects model examining the interactive effects of
 795 THg ($\mu\text{g/g}$ dry weight), $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) as well as an interaction between body mass (g) and
 796 clutch size on prolactin (PRL) levels (ng/mL). The breeding colony (n=6) of the 106 female
 797 arctic-breeding common eiders throughout Canada and Eurasia was a random variable in the
 798 model, with the John's Island eiders and 12 additional individuals from other colonies removed
 799 from the model due to the absence of morphometrics (significant p-values are bolded).

	Estimate	Standard Error	df	t-value	p-value
Intercept	306.746	19.540	4.526	15.599	<0.001
Body Mass	-9.472	7.375	93.941	-1.284	0.202
Clutch Size	4.628	6.389	94.890	0.724	0.471
Mass*Clutch	-0.36	6.872	92.220	-0.053	0.958
THg	-7.108	9.509	93.910	-0.747	0.457
$\delta^{13}\text{C}$	-17.543	11.313	77.172	-1.551	0.125
$\delta^{15}\text{N}$	25.427	11.107	80.279	2.289	0.025
THg* $\delta^{13}\text{C}$	7.484	8.609	94.777	0.869	0.387
THg* $\delta^{15}\text{N}$	6.437	5.918	94.889	1.088	0.280
$\delta^{15}\text{N}$ * $\delta^{13}\text{C}$	-13.376	10.882	92.772	-1.229	0.222
THg*$\delta^{15}\text{N}$*$\delta^{13}\text{C}$	14.138	6.767	94.561	2.089	0.039

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802

Figure 1. Locations of the seven pan-Arctic and subarctic common eider colonies used in this

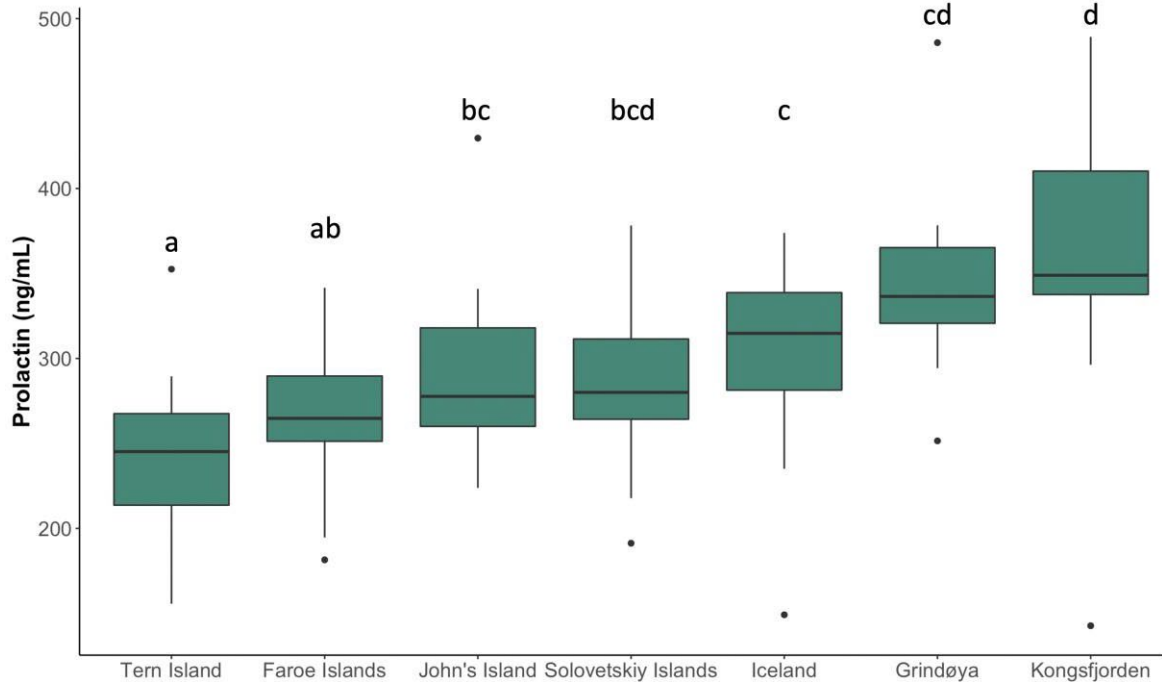
803

study (stars). Colonies are numbered by descending median colony PRL levels (1=highest,

804

7=lowest). Map provided by naturalearthdata.com.

805



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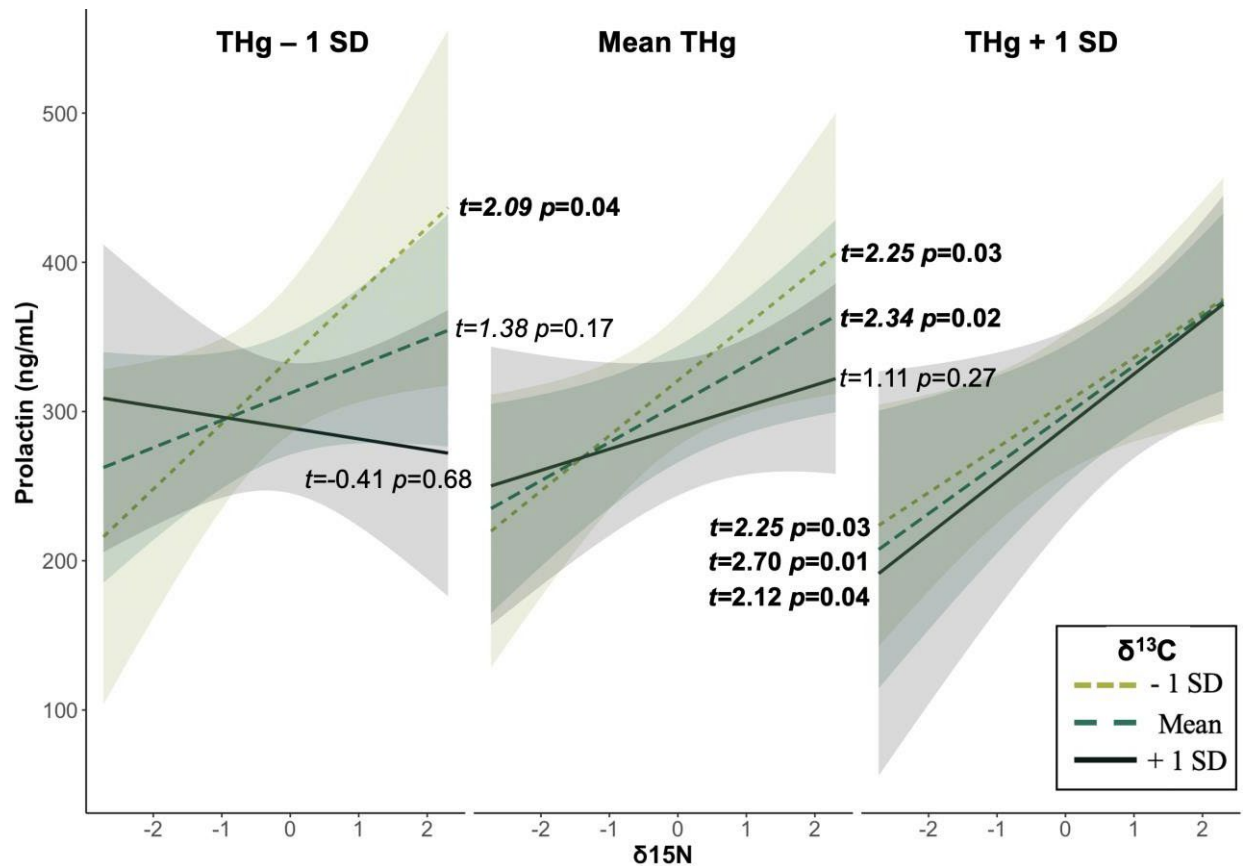
807 **Figure 2.** Boxplot depicting whether the mean PRL levels at each common eider colony vary

808 significantly. Significance was determined using a one-way ANOVA at an alpha of 0.05 and a

809 posthoc Tukey test using the R package car v.3.0-10. Letters above each colony show whether a

810 colony significantly differs from the others, where the absence of shared letters indicates

811 significant difference in mean PRL levels between locations.



812

813 **Figure 3.** Interactive effect of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg (visualized using standard deviation from the

814 mean; SD) on PRL levels in 106 incubating common eiders combined from six pan Arctic

815 breeding colonies. The model used for this analysis included eider colony as a random variable.

816 Values for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg are without units as they are derived from standardized model

817 output for simplicity using the R package Interactions version 1.1.3. Shaded areas represent a

818 95% confidence interval for each slope. Slopes that are significantly different from zero, as

819 determined by Johnson-Neyman simple slopes analysis, are bolded.

Do foraging ecology and contaminants interactively predict parenting hormone levels in common eider?

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