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1 Sex- and age-specific mercury accumulation in a long-lived seabird

2

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14

15 **Abstract**

16 Mercury levels in the environment are increasing, such that they are also expected to accumulate in top-  
17 predators, but individual-based longitudinal studies required to investigate this are rare. Between 2017  
18 and 2023, we therefore collected 1314 blood samples from 588 individual common terns (*Sterna*  
19 *hirundo*) to examine how total blood mercury concentration changed with age, and whether this differed  
20 between the sexes. Blood mercury concentrations were highly variable, but all exceeded toxicity  
21 thresholds above which adverse health effects were previously observed. A global model showed blood  
22 mercury to be higher in older birds of both sexes. Subsequent models partitioning the age effect into  
23 within- and among-individual components revealed a linear within-individual accumulation with age in  
24 females, and a decelerating within-individual accumulation with age in males. Time spent at the  
25 (particularly contaminated) breeding grounds prior to sampling and laying in females were also found  
26 to affect mercury concentrations. As such, our study provides evidence that male and female common  
27 terns differentially accumulate mercury in their blood as they grow older and calls for further studies of  
28 the underlying mechanisms as well as its consequences for fitness components, such as reproductive  
29 performance and survival.

30

31 **Keywords**

32 THg, pollution, plasticity, ageing, phenology, longitudinal study

33

## 34 **Introduction**

35 Industrial activities and other drivers of global change, such as ongoing climate warming, increase  
36 environmental mercury levels (Fitzgerald et al., 2007; Eagles-Smith et al., 2018; UN Environment,  
37 2019). As mercury enters aquatic ecosystems, microorganisms transform it into its organic and  
38 bioavailable form, methylmercury (MeHg). When biota ingest methylmercury, it can accumulate along  
39 the food chain (Atwell et al., 1998), exposing long-lived top predators, such as some seabird species, to  
40 particularly high levels. As such, seabirds have sometimes been used as bioindicators to monitor  
41 environmental mercury contamination and to study its consequences for physiology, behaviour and  
42 fitness components (Burger and Gochfeld, 2004). Blood is a tissue regularly used for this purpose, as it  
43 enables the measurement of an individual bird's mercury contamination without sacrificing it (Kahle  
44 and Becker, 1999). It additionally provides an opportunity for repeated sampling of the same individuals.

45 Repeated blood sampling of seabirds is most feasible during the breeding season, when  
46 individuals are usually highly site faithful and can be caught and/or sampled during nest attendance on  
47 land. Blood mercury levels during the breeding season largely reflect a combination of recent mercury  
48 uptake, dependent on trophic position and contamination of prey items in the main foraging areas  
49 (Monteiro and Furness, 1995), and levels of deposition in internal organs (Eagles-Smith et al., 2008;  
50 Fromant et al., 2016). For migratory seabirds, however, there may also be carry-over effects from  
51 mercury uptake in the wintering areas or during migration (Lavoie et al., 2014; Quillfeldt et al., 2022;  
52 Carravieri et al., 2023), the influence of which could depend on the timing of sampling relative to the  
53 timing of these other events along the annual cycle (Eagles-Smith et al., 2009a).

54 Besides by timing, local uptake and deposition in internal tissues, blood mercury contamination  
55 may be affected by sex. Female birds have often been found to exhibit lower mercury levels than males,  
56 potentially suggesting a role for egg laying in the ability of females to excrete part of their mercury  
57 (Bond and Diamond, 2009; Ackerman et al., 2020; but see Robinson et al., 2012; Hitchcock et al., 2019).  
58 To test whether egg laying could explain (part of) the observed sex difference, one would ideally sample  
59 birds of both sexes both prior to, and after, female egg laying, or artificially manipulate the number of  
60 eggs females produce, for example by conducting an egg removal experiment, inducing females to

61 produce additional eggs. Alternatively, however, one could test whether variation in clutch size explains  
62 variation in post-laying levels of mercury contamination in both sexes, whereby one would expect a  
63 negative correlation in females only in case of eggs being a pathway for detoxification.

64 Despite detoxification, potentially via eggs in females (Bond and Diamond, 2009; Ackerman et  
65 al., 2020), and via feathers in birds of both sexes (>90%; Braune and Gaskin, 1987a; Whitney and  
66 Cristol, 2017), if incomplete, the relative longevity of seabirds might predispose them to  
67 bioaccumulation of mercury as they age (Rowe, 2008; Celik et al., 2021). Studies examining the age-  
68 specificity of mercury contamination in birds have, however, not yet yielded conclusive evidence for  
69 this to occur. Insightful first studies reported the expected positive correlation between age and mercury  
70 concentration when comparing birds of different age classes, i.e. chicks vs. adults (Souza et al., 2020;  
71 Bighetti et al., 2021). Given that chicks and adults do not only differ in age, but may also differ in diet  
72 - with chicks feeding on smaller, potentially less contaminated prey items - and moult pattern - given  
73 that chicks are in the process of growing their feathers, potentially depositing mercury - these results,  
74 however, do not provide conclusive proof that mercury accumulates as birds grow older. Indeed, among  
75 adult seabirds, further studies found either no (Thompson et al., 1993; Becker et al., 2002; Carravieri et  
76 al., 2014, 2022; Tartu et al., 2015) or a negative correlation (Agusa et al., 2005; Tavares et al., 2013;  
77 Tartu et al., 2014) between age and mercury concentration. Interpretation of the differences in the  
78 perhaps surprising results among these latter studies is currently hampered by the fact that all were based  
79 on cross-sectional data, which do not facilitate distinguishing between within-individual accumulation  
80 of mercury with age and among-individual variation in survival in relation to mercury pollution level  
81 (selective disappearance, *sensu* van de Pol and Wright, 2009). Mercury levels could, for example, be  
82 positively associated with survival due to better foragers both acquiring more resources to aid survival  
83 (as a function of individual quality), but also becoming more contaminated via increased dietary mercury  
84 uptake (Binkowski et al., 2021). Alternatively, mercury levels could be negatively associated with  
85 survival (Ma et al., 2018a) due to detrimental effects on physiology (Hawley et al., 2009; Lewis et al.,  
86 2013; Ma et al., 2018a, 2018b; Adams et al., 2020; Grunst et al., 2023a). Such selective disappearance  
87 would result in patterns of age-specific mercury contamination at the population level (here: an in- or  
88 decrease, respectively) that could either mask or inflate within-individual patterns of accumulation.

89 When data have been collected longitudinally, methods are available to assess the relative importance  
90 of within- and among-individual sources of age-related patterns of mercury contamination (van de Pol  
91 and Wright, 2009). These methods have been routinely applied in studies of ageing in birds (see  
92 Bouwhuis and Vedder, 2017 for a review), and could be useful when adopted in studies of avian  
93 physiology as well.

94 In this study, we assess factors underlying variation in blood mercury concentrations in a long-  
95 lived migratory seabird, the common tern (*Sterna hirundo*). Using 1209 blood samples obtained from  
96 588 common terns of known age and sex, and collected across seven years, we investigate whether  
97 variation in total mercury levels (THg) can be explained by the birds' (i) timing, assessed as the intervals  
98 between arrival at the breeding colony, egg laying and blood sampling, (ii) sex, (iii) clutch size and (iv)  
99 age. Importantly, after first running a global linear mixed effect model assessing the effect of age, we  
100 adopt a longitudinal analysis approach and run a second linear mixed effect model to test whether age-  
101 specificity of mercury concentration is best explained by within-individual processes and/or selective  
102 (dis)appearance of birds in relation to, or based on, their mercury levels. Third, we add a within-season  
103 perspective to our analyses, enabled by the fact that 88 birds were sampled repeatedly either within a  
104 single breeding attempt or among two breeding attempts when birds re-nested after having failed.

105

## 106 **Methods**

### 107 **Study species and site**

108 Common terns are long-lived seabirds, mainly feeding on fish of a length up to 15 cm (Becker and  
109 Ludwigs, 2004). After migration to their wintering areas along the African coast (Kürten et al., 2022),  
110 they return to their breeding colony each spring (Dittmann and Becker, 2003; Dittmann et al., 2005).  
111 Starting their first breeding attempt on average at an age of three years, common terns usually produce  
112 clutches of one to three eggs, which are incubated by both pair members (Becker and Ludwigs, 2004).  
113 Their colonial breeding, longevity and high level of site-fidelity (Szostek and Becker, 2012) make  
114 common terns particularly suitable for extensive longitudinal studies.

115 We studied the mercury concentration in blood of common terns breeding at a monospecific  
116 colony located at the Banter See in Wilhelmshaven, at the German North Sea coast (53°30'40" N,  
117 08°06'20" E). Since 1992, this colony is monitored three times weekly to, among others, record laying  
118 date and clutch size for each nest, and all locally hatched birds are marked with rings as well as  
119 subcutaneously implanted transponders if they reach fledging age (Becker and Wendeln, 1997). The  
120 colony site consists of six artificial islands (10.7 x 4.6 m), covered with gravel and surrounded by 60 cm  
121 high walls. The walls sustain 44 resting platforms equipped with antennas that allow the automatic and  
122 remote detection of arrival date (Moiron et al., 2020) and presence of transponder-marked birds.  
123 Additionally, placing mobile antennas around each nest for at least 24 hours allows the identification of  
124 breeders and linking them to their nests. The sex of the studied birds is determined molecularly following  
125 Becker and Wink (2003).

126

### 127 **Blood collection**

128 Between May and August 2017 – 2023, we used the antenna system to identify 588 transponder-marked  
129 common terns during incubation to collect 1209 blood samples 3 – 36 days after the first egg of their  
130 clutch was laid. We collected 47 further blood samples from 45 birds within the same breeding attempt  
131 within 1 – 24 days after their first blood collection in 2021 and 2023. Despite replacement clutches being  
132 infrequent (approximately 9%), they significantly contribute to the lifetime reproductive success of  
133 common terns (Becker and Zhang, 2011) and we made use of their occurrence to additionally collect 58  
134 blood samples from 55 individuals within 19 – 55 days after their first blood collection in 2017, 2021,  
135 2022 and 2023 (Table 1). In all cases, blood sampling was conducted prior to hatching of the first chick.  
136 In total, we collected 1314 blood samples from 588 individuals (Table 1).

137 For blood sampling, we used starved kissing bugs (*Dipetalogaster maxima*; Becker et al., 2006).  
138 We inserted one or two third larval instars into an artificial hollow egg, closely resembling real common  
139 tern eggs in size and colour. After the target bird was detected on its nest by the automatic antenna  
140 system, we replaced one of its real eggs with the “bug-egg”, storing the real egg in a foam-lined box  
141 kept warm in an incubator at 37°C. Birds resumed incubation shortly after nest manipulation. Small

142 holes along the artificial egg allowed the bug(s) to suck blood from the incubating bird. Throughout this  
 143 process, birds were meticulously observed from observation huts within the colony to prevent sample  
 144 contamination by switches between partners. After 20 – 30 minutes, we visually confirmed whether the  
 145 bug had successfully obtained a blood meal; if so, we retrieved the artificial egg and returned the real  
 146 egg. Up to 500µl blood of the bird was then extracted from the bug's abdomen using a syringe and stored  
 147 at -18°C until analysis. To ensure that mercury concentrations in blood sampled this way are not affected  
 148 by bug physiology, in 2017, we additionally blood sampled 18 birds (7 males and 11 females) from the  
 149 brachial vein using needles and capillaries. A correlation test, performed in R, showed a highly  
 150 significant correlation of 0.93 (Fig. S1).

151

152 **Table 1: Details regarding the 1314 blood samples collected from 588 incubating common terns in the years**  
 153 **2017 – 2023 (total (males; females)).**

| Year  | No of 1st blood samples taken | No of 2nd blood samples taken within the same clutch | No of 2nd blood samples taken from a replacement clutch |
|-------|-------------------------------|--|---|
| 2017  | 157 (78; 79)                  | -  | 5 (2; 3)  |
| 2018  | 166 (78; 88)                  | -  | -   |
| 2019  | 216 (106; 110)                | -  | -   |
| 2020  | 107 (51; 56)                  | -  | -   |
| 2021  | 152 (73; 79)                  | 26 (13; 13)  | 30 (14; 16)   |
| 2022  | 184 (97; 87)                  | -  | 11 (7; 4)   |
| 2023  | 227 (114; 113)                | 21 (8; 13)   | 12 (7; 5)   |
| total | 1209 (597; 612)               | 47 (21; 26)  | 58 (30; 28)   |

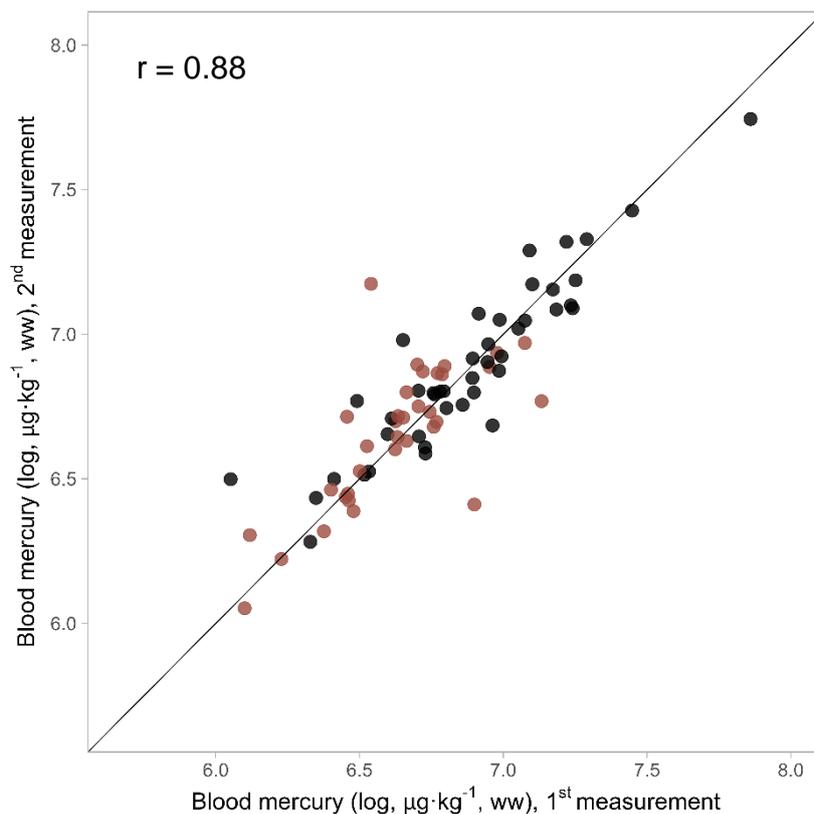
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### 155 **Mercury analysis**

156 Mercury analysis was performed using a Direct Mercury Analyzer (DMA-80, MLS Mikrowellen-Labor-  
 157 Systeme GmbH, Germany) to quantify total mercury concentration (THg), which we report on a wet-  
 158 weight (ww) basis, and which provides a reliable proxy for MeHg levels (Renedo et al., 2021). For each  
 159 sample, ca. 20 µl of wet whole blood was pipetted into a nickel sample boat and weighted, then dried

160 and thermally decomposed in a stream of oxygen at 750 °C. This process released gaseous mercury that  
161 was trapped by gold amalgamation to prevent its combustion along with the remaining compounds of  
162 the blood sample. By subsequent heating to 850°C, the mercury was released and determined by atomic  
163 absorption spectrometry at 253.7 nm. Each of our 35 measurement batches included an analytical blank  
164 to verify the absence of contamination of the device and for 29 out of the 35 od the batches we have the  
165 values obtained for a certified reference material (DORM-4; fish protein from National Research  
166 Council, Canada, 412  $\mu\text{g}\cdot\text{kg}^{-1}$  dry weight; with a mean percent recovery  $\pm$  standard deviation of  $109 \pm$   
167 7%) to ensure its accuracy as well. The detection limit of THg was  $0.0003 \mu\text{g}\cdot\text{g}^{-1}$  and none of the samples  
168 showed a value below this limit.

169 As part of the laboratory's quality assurance and quality control (QA/QC) measures, it engages  
170 in the QUASIMEME international laboratory performance study program twice a year with satisfactory  
171 results. Nevertheless, to evaluate the reliability of our measurement method, we split 77 sufficiently  
172 large blood samples to obtain duplicates, which were measured blindly and across batches. The relative  
173 difference among duplicates was  $10 \pm 11\%$  and a correlation test, using the cor.test function in R, showed  
174 a highly significant correlation of 0.88 (Fig. 1), such that all further samples were measured only once.



176

177

178 **Figure 1:** Correlation between two total blood mercury concentration measurements of the same blood sample (n  
179 = 43 male samples in black, 34 female samples in red). The line represents the x = y line, the slope of the correlation  
180 between both equals  $0.82 \pm 0.05$  SE.

181

## 182 **Statistical analyses**

183 To assess potential sources of variation in the blood THg levels of common terns, we first used a linear  
184 mixed model with ‘blood THg concentration’ (in  $\mu\text{g}\cdot\text{kg}^{-1}$  ww) as the dependent variable and ‘year’ and  
185 ‘individual identity’ as random effects to account for the non-independence of repeated observations on  
186 the same individual and potential environmental fluctuations across years. We  $\log_e$ -transformed our  
187 dependent variable to meet model assumptions. We included ‘age’ as a linear and a quadratic covariate,  
188 and ‘sex’ as 2-level and ‘clutch size’ as 3-level class variables, to not limit ourselves to assuming linear  
189 effects. To account for the fact that common terns are migratory, and that the sampled individuals may  
190 have taken different amounts of time to transfer from arriving to laying the first egg (Moiron et al.,  
191 2023), we added the ‘interval between arrival and laying date’ as a covariate. Moreover, we added the  
192 ‘interval between laying and sampling’ as another covariate to correct for any potential methodological  
193 variation in the speed with which we could sample birds in the field (which mainly depends on the  
194 synchrony of breeding). Finally, we tested for sex-specificity of our candidate variables by including all  
195 interactions between ‘sex’ and the terms introduced above.

196 Given our finding of age-specificity of blood mercury levels (see Results and Table S1), we ran a second  
197 linear mixed model where used a within-subject age standardization to separate within- and among-  
198 individual age effects. Hereto, we partitioned the age of each individual into an ‘average age’ and ‘delta  
199 age’ component (following van de Pol and Wright, 2009). An individual’s average age was calculated  
200 as the average of all ages at which the bird was sampled, while delta age was calculated as the difference  
201 between an individual’s actual age at sampling and its average age (i.e., ‘delta age’ = ‘actual age’ –  
202 ‘average age’, see Table S2 for an example). When including both ‘average age’ and ‘delta age’ as

203 covariates in the model, ‘average age’ quantifies the among-individual age effect, whereas ‘delta age’  
204 quantifies the within-individual change in THg concentration as birds grow older (van de Pol and  
205 Wright, 2009). If the among- and within-individual age effects were to be significantly different from  
206 each other, this would indicate that the effect of age among individuals cannot be explained by changes  
207 within individuals, meaning that there is age-specific selective (dis)appearance of individuals with  
208 certain levels of THg concentrations from the sampled pool of individuals (van de Pol and Wright,  
209 2009). In addition to the main effects of ‘average age’ and ‘delta age’, we added the interaction between  
210 them to test for non-linearity of any within-individual change in THg concentration with age, such as  
211 accelerating or decelerating effects as birds grow older. Finally, as in the first model, we tested for sex-  
212 specificity of our candidate variables by including all interactions between ‘sex’ and the introduced  
213 terms, as well as the three-way interaction between ‘average age’, ‘delta age’ and ‘sex’. Candidate  
214 variables were not highly correlated (Fig. S2), such that we were able to enter them simultaneously.

215           Given that we found a significant interaction between ‘sex’ and ‘interval between arrival and  
216 laying date’ (in both the first and second model, see Results and Table S1), we proceeded to run the  
217 second model for males and females separately, excluding the interactions with sex as well as the main  
218 effect of sex (Table 2b and c). In addition, we repeated these sex-specific models while replacing ‘delta  
219 age’ by the ‘actual age’ of an individual, to test whether the ‘average age’ and ‘delta age’ effects were  
220 significantly different from one another (van de Pol and Wright, 2009), which would indicate selective  
221 (dis)appearance of birds with low or high THg levels (see above, Tables 2b and c).

222           To determine how two THg concentrations obtained from the same bird in the same season  
223 correlate, we ran a final linear mixed model with the log<sub>e</sub>-transformed ‘second blood THg concentration’  
224 as the dependent variable and the ‘first blood THg concentration’ as a covariate. As above, ‘individual  
225 identity’ and ‘year’ were included as random effects. ‘Clutch’ of the second sample (same or  
226 replacement) and ‘sex’ were included as 2-level class variables. Additionally, we added the interaction  
227 between (i) ‘clutch’ and ‘sex’ to test whether the fact that females laid eggs in between the two  
228 measurements in cases where the second sample was taken while the birds were incubating their  
229 replacement clutch made a difference, as well as (ii) ‘clutch’ and ‘first blood THg concentration’ to  
230 account for the fact that the temporal interval between the two measurements was larger in cases where

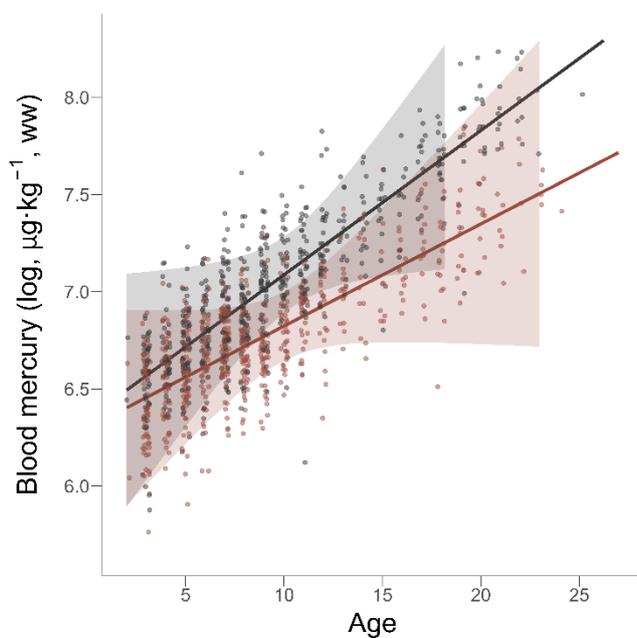
231 the second sample was taken while the birds were incubating a replacement clutch. Further, we included  
232 the three-way interaction between ‘clutch’, ‘sex’ and ‘first blood THg concentration’ because we  
233 expected the correlation to be stronger for males than females in cases when the clutch was different,  
234 but not when the clutch was the same.

235 All analyses were performed and figures created, using R (version 4.3.1, R Core Team 2022).  
236 Models were run with the R package “lme4” (Bates et al., 2015). P-values were obtained using the  
237 package “lmerTest” (Kuznetsova et al., 2017) with the level of significance set at  $p < 0.05$ . Data were  
238 visualized using the R packages “ggplot2” (Wickham, 2016) or “interactions” (Long, 2022).

239

## 240 Results

241 The total mercury concentration (THg) in 1209 blood samples collected from 588 individual common  
242 terns ranged from 0.29 to 3.90  $\mu\text{g}\cdot\text{g}^{-1}$  ww, with a mean  $\pm$  SE of  $1.00 \pm 0.11$ . Part of this variation was  
243 explained by significant positive linear and negative quadratic age effects, with older birds exhibiting  
244 higher THg concentrations in their blood than younger birds (Table S1, Fig. 2).



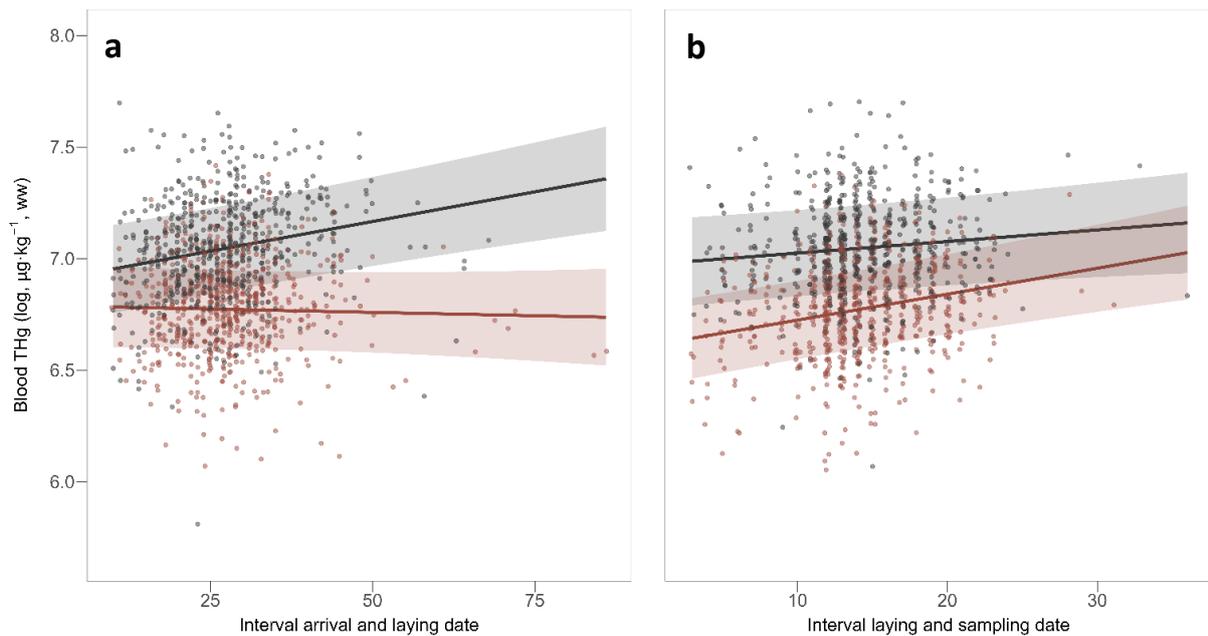
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246 **Figure 2:** Total blood mercury concentrations of common terns in relation to age. Each point represents  
247 the partial residual of a blood sample (black = males, red = females), lines the sex-specific linear  
248 regressions and shaded areas the confidence interval.

249 To distinguish between within-individual accumulation of mercury with age and among-individual  
250 variation in survival in relation to mercury pollution level driving the observed age effect, we repeated  
251 the model splitting age into average and delta age components. This model showed that part of the  
252 variation in the terns' blood THg concentrations was explained by a significant interaction between sex  
253 and 'interval between arrival and laying date', with the interaction between sex and 'interval between  
254 laying and sampling date' and the three-way-interaction between sex, average age and delta age also  
255 being close to significance (Table 2a), such that we subsequently ran sex-specific models to assess  
256 effects for males and females separately.

257 The sex-specific model for females showed that there was no correlation between the interval  
258 between arrival and laying of the first egg and female THg concentration (Fig. 3a, Table 2b), but that  
259 THg levels were higher in females with a longer interval between first egg laying and blood sampling  
260 (Fig. 3b). In addition, females that laid three eggs had significantly lower THg levels than those that laid  
261 one egg, with females laying two eggs showing an intermediate THg level that was not significantly  
262 different from either (Fig. S3). Females with a higher average age had higher THg levels than those with  
263 a lower average age (Fig. 2), which most likely can be explained by within-individual accumulation of  
264 THg with age, given that the within-individual term for delta age showed a trend towards being positive  
265 (Fig. 4) and the within- and among-individual estimates not differing from one another, such that  
266 selective (dis)appearance in relation to THg should not be underlying variation among females.

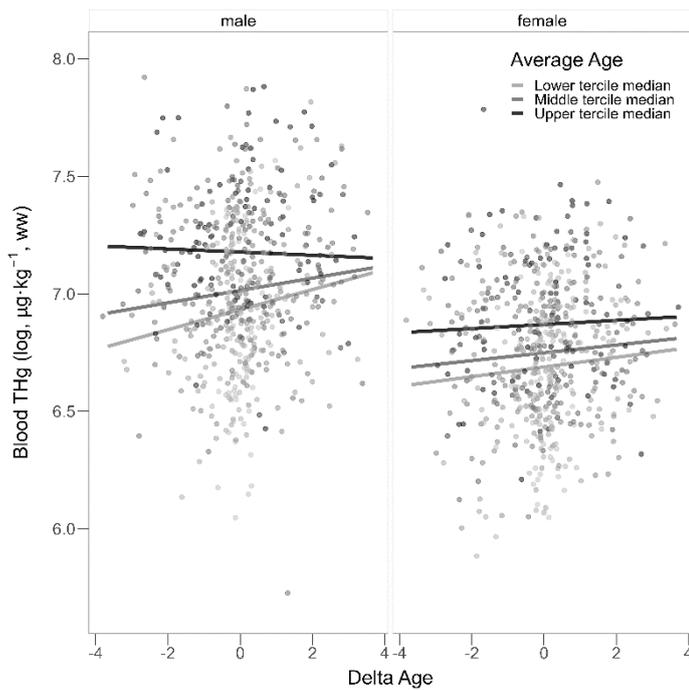
267



268 **Figure 3:** Total blood mercury concentration of male (black) and female (red) common terns in relation to their  
 269 (a) interval between arrival and laying date and (b) interval between laying and sampling date, both in days. Each  
 270 point represents the partial residual of a blood sample, lines the sex-specific linear regressions, shaded areas the  
 271 confidence intervals.

272

273 The sex-specific model for males showed significantly positive correlations between the interval  
 274 between arrival and laying (by their partner) and the interval between laying (by their partner) and blood  
 275 sampling and male THg levels (Fig. 3a and b, Table 2c). Additionally and interestingly, THg levels were  
 276 lower in males whose partner laid a larger clutch, although not significantly so (Fig. S2). Similar to  
 277 females, THg levels in the blood of older males were higher than those in younger ones (Fig. 2), which  
 278 can be attributed to a significant within-individual accumulation, although one that in males decelerated  
 279 with age (Fig. 4), given that the within- and among-individual patterns did not differ from one another,  
 280 but did show a significant interaction.

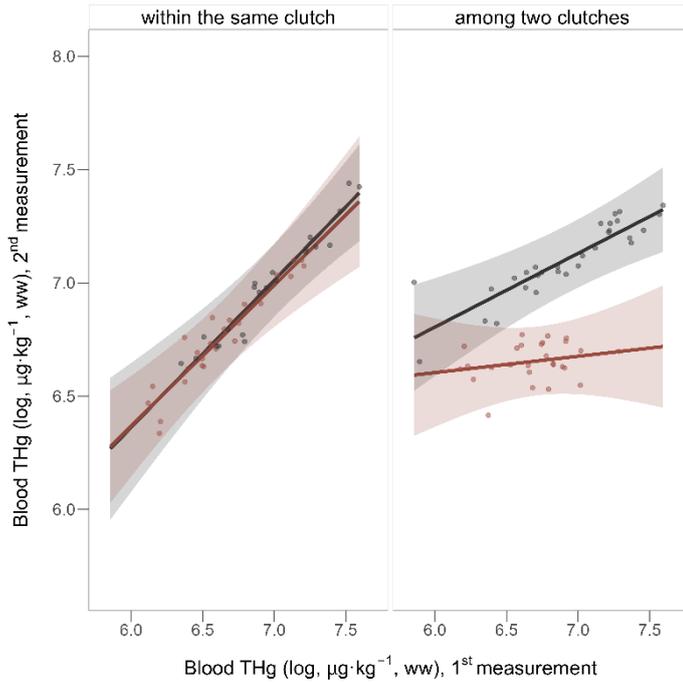


281

282 **Figure 4:** Total blood mercury concentration of male (left) and female (right) common terns in relation to the age,  
 283 in years, at which they were sampled relative to the average age at which they were sampled ('delta age'). Each  
 284 point represents the partial residual of a blood sample; lines the predicted within-individual change across seven  
 285 years for birds sampled at an average age at the lower (5 years), middle (8 years) and upper (14 years) tercile  
 286 median (from light grey to black), respectively.

287

288 Our within-season analysis revealed that variation in the THg concentration at the second  
 289 measurement within a season can be explained by a significant interaction between clutch and THg  
 290 concentration at the first measurement, with there being a trend towards this interaction differing  
 291 between the sexes (Table 3). These interactions show that the correlation between the two THg  
 292 concentrations is stronger when measured within the same clutch, especially for females (Fig. 5).



293

294 **Figure 5:** Total blood mercury concentration at the second sampling event within a season, either within the same  
 295 clutch (n=47, left) or among two clutches (n=58, right). Each point represents the partial residual of a second blood  
 296 sample (black = males, red = females), lines the linear regression for each sex and shaded areas the confidence  
 297 intervals.

298

299 **Table 2: Results from three models testing whether selected candidate factors explain variation in (log-**  
 300 **transformed) blood total blood mercury concentrations ( $\mu\text{g}\cdot\text{kg}^{-1}\text{ ww}$ ) of 1209 samples taken from 588**  
 301 **common terns for (a) both sexes combined, (b) females, and (c) males.**

| Dependent variable      | Estimate $\pm$ SE  | t-value | p-value        |
|-------------------------|--------------------|---------|----------------|
| (a) both sexes (n=1209) |                    |         |                |
| Intercept               | 6.577 $\pm$ 0.1097 | 59.977  | < <b>0.001</b> |
| Sex (female)            | -0.137 $\pm$ 0.105 | -1.306  | 0.192          |
| Clutch size (2)         | -0.107 $\pm$ 0.066 | -1.613  | 0.107          |
| Clutch size (3)         | -0.095 $\pm$ 0.066 | -1.449  | 0.148          |
| Interval AD – LD        | 0.005 $\pm$ 0.001  | 4.611   | < <b>0.001</b> |
| Interval LD - SD        | 0.005 $\pm$ 0.002  | 2.119   | <b>0.034</b>   |
| Average age             | 0.027 $\pm$ 0.003  | 9.821   | < <b>0.001</b> |

|                                    |                |        |                |
|------------------------------------|----------------|--------|----------------|
| Delta age                          | 0.070 ± 0.020  | 3.523  | < <b>0.001</b> |
| Sex (female)*clutch size (2)       | 0.010 ± 0.084  | 0.119  | 0.905          |
| Sex (female)*clutch size (3)       | -0.015 ± 0.083 | -0.186 | 0.853          |
| Sex (female)*interval AD – LD      | -0.006 ± 0.002 | -3.661 | < <b>0.001</b> |
| Sex (female)*interval LD – SD      | 0.006 ± 0.003  | 1.877  | 0.061          |
| Sex (female)*average age           | -0.007 ± 0.004 | -1.853 | 0.064          |
| Sex (female)*delta age             | -0.043 ± 0.026 | -1.654 | 0.099          |
| Average age*delta age              | -0.005 ± 0.002 | -3.322 | < <b>0.001</b> |
| Sex (female)*average age*delta age | 0.004 ± 0.002  | 1.862  | 0.063          |

Variance ± SD

|              |               |
|--------------|---------------|
| Year (r)     | 0.038 ± 0.196 |
| Identity (r) | 0.020 ± 0.144 |
| Residual (r) | 0.044 ± 0.211 |

(b) females (n=612)

---

|                            |                |        |                |
|----------------------------|----------------|--------|----------------|
| Intercept                  | 6.459 ± 0.098  | 66.211 | < <b>0.001</b> |
| Clutch size (2)            | -0.092 ± 0.050 | -1.850 | 0.065          |
| Clutch size (3)            | -0.106 ± 0.050 | -2.137 | <b>0.033</b>   |
| Interval AD – LD           | -0.001 ± 0.001 | -0.740 | 0.460          |
| Interval LD – SD           | 0.011 ± 0.002  | 4.589  | < <b>0.001</b> |
| Average age                | 0.020 ± 0.003  | 7.520  | < <b>0.001</b> |
| Delta age                  | 0.033 ± 0.018  | 1.799  | 0.073          |
| Average age*delta age      | -0.002 ± 0.002 | -1.017 | 0.310          |
| Average age (sel. d. app.) | 0.022 ± 0.011  | 0.211  | 0.833          |
| Actual age (sel. d. app.)  | 0.017 ± 0.010  | 1.748  | 0.081          |

Variance ± SD

|              |               |
|--------------|---------------|
| Year (r)     | 0.034 ± 0.183 |
| Identity (r) | 0.016 ± 0.125 |

Residual (r) 0.043 ± 0.207

(c) males (n=597)

---

|                            |                |        |                |
|----------------------------|----------------|--------|----------------|
| Intercept                  | 6.564 ± 0.116  | 56.629 | < <b>0.001</b> |
| Clutch size (2)            | -0.116 ± 0.068 | -1.699 | 0.090          |
| Clutch size (3)            | -0.107 ± 0.068 | -1.578 | 0.115          |
| Interval AD – LD           | 0.005 ± 0.001  | 4.507  | < <b>0.001</b> |
| Interval LD – SD           | 0.006 ± 0.003  | 2.232  | <b>0.026</b>   |
| Average age                | 0.028 ± 0.003  | 9.184  | < <b>0.001</b> |
| Delta age                  | 0.065 ± 0.021  | 3.144  | <b>0.002</b>   |
| Average age*delta age      | -0.005 ± 0.002 | -3.131 | <b>0.002</b>   |
| Average age (sel. d. app.) | 0.018 ± 0.011  | 1.595  | 0.111          |
| Actual age (sel. d. app.)  | 0.009 ± 0.011  | 0.874  | 0.382          |

Variance ± SD

Year (r) 0.044 ± 0.210

Identity (r) 0.027 ± 0.164

Residual (r) 0.045 ± 0.213

302

303 Significant results ( $p < 0.05$ ) are presented in bold. ‘Average age (sel. d. app.)’ and ‘Actual age (sel. d. app.)’, both  
304 in years, report the results for the analysis in which we test whether the average and delta age estimates obtained  
305 in the main model are significantly different from one another; all other results reported are obtained from the  
306 main model in which ‘average age’ and ‘delta age’, also in years, and their interaction are included. ‘Interval AD  
307 – LD’ represents the interval between arrival and laying date, ‘Interval LD – SD’ the interval between laying and  
308 sampling date, both in days. Clutch size refers to the size of the clutch the bird was incubating while its blood  
309 sample was collected.

310

311 **Table 3: Results from a model testing whether clutch (same or replacement), sex and/or log<sub>e</sub>-transformed**  
 312 **first total blood mercury concentration explain variation in the (log<sub>e</sub>-transformed) second total blood**  
 313 **mercury concentrations (µg·kg<sup>-1</sup> ww) of 88 common terns sampled multiple times within a season.**

| Dependent variable   | Estimate ± SE  | t-value | p-value          |
|--|----------------|---------|------------------|
| Intercept  | 2.466 ± 0.832  | 2.964   | <b>0.004</b>     |
| Clutch (replacement)                                       | 2.387 ± 0.878  | 2.718   | <b>0.009</b>     |
| First Hg concentration                                     | 0.649 ± 0.118  | 5.488   | <b>&lt;0.001</b> |
| Sex (female)   | 0.171 ± 1.086  | 0.158   | 0.875            |
| Clutch (replacement)*first THg concentration               | -0.324 ± 0.124 | -2.604  | <b>0.013</b>     |
| Clutch (replacement)*sex (female)                          | 1.147 ± 1.443  | 0.795   | 0.430            |
| Clutch (replacement)* first THg concentration*sex (female) | -0.028 ± 0.159 | -0.173  | 0.863            |
| Clutch (replacement)* first THg concentration*sex (female) | -0.253 ± 0.151 | -1.677  | 0.099            |
|  | Variance ± SD  |         |                  |
| Year (r)   | 0.017 ± 0.131  |         |                  |
| Identity (r)   | 0.026 ± 0.161  |         |                  |
| Residual (r)   | 0.013 ± 0.115  |         |                  |

314 Significant results (p < 0.05) are presented in bold.

315

### 316 **Discussion**

317 In this study, we used seven years of longitudinal data to assess factors underlying variation in total  
 318 mercury concentration (THg) in the blood of a long-lived seabird, the common tern. THg concentrations  
 319 were highly variable, ranging from 0.29 to 1.80 µg·g<sup>-1</sup> ww in females and from 0.35 to 3.90 µg·g<sup>-1</sup> ww  
 320 in males, showing an overall mean of 1.00 ± 0.11 µg·g<sup>-1</sup> ww.

321 Apart from the overall difference in blood THg concentrations between male and female  
 322 common terns, we observed differences between the sexes in the correlations between some of our

323 variables of interest and THg concentrations (Table 2a). Consequently, we ran sex-specific analyses.  
324 With respect to phenology, for males, the sex-specific analysis showed that males with longer intervals  
325 between arrival and the onset of laying by their female, and between laying and sampling had higher  
326 blood THg levels (Table 2c). This may suggest that a longer time spent at the breeding area results in  
327 males being exposed to a higher dietary uptake of methylmercury (MeHg) compared to the uptake in  
328 their foraging areas prior to arrival. This seems supported by a recent study showing an increasing  
329 temporal trend in mercury contamination of fish in this area (Kammann et al., 2023). Alternatively or  
330 additionally, however, the causality may be reversed, such that males with higher THg levels might have  
331 arrived in a poorer condition, for example due to MeHg exacerbating oxidative stress (Hoffman et al.,  
332 2011; Costantini et al., 2014; Eckbo et al., 2019; Soldatini et al., 2020) and/or hormone levels (Varian-  
333 Ramos et al., 2014), resulting in delayed breeding and/or reduced incubation behaviour, leading to us  
334 needing longer to sample them successfully.

335 In females, there was no correlation between the interval between arrival and egg laying and  
336 THg concentrations, while the correlation between the interval between laying and sampling and THg  
337 concentrations was significantly positive (Table 2b) and showed a trend towards being slightly stronger  
338 than in males (Table 2a). This difference between the sexes might be explained by females' ability to  
339 reduce mercury concentrations via egg laying (Bond and Diamond, 2009; Ackerman et al., 2020). If a  
340 longer time spent at the breeding area indeed results in higher blood THg concentrations due to high  
341 environmental contamination, egg laying could initially offset an increase in blood THg concentrations  
342 in females, but not males. However, after clutch completion, this additional excretion mechanism would  
343 cease, leading to an increase in female THg levels over time as well. This hypothesis is supported by  
344 our results obtained from the repeated THg measurements within breeding seasons. Whereas the within-  
345 individual correlation between THg concentrations is similarly positive for the sexes if both  
346 measurements were obtained from blood samples taken within a single clutch, it is somewhat weaker  
347 for females than males if the second blood sample was taken during incubation of a replacement clutch,  
348 most likely due to a repeated reduction of THg levels by females through egg laying.

349 A considerable role of egg laying for female THg detoxification is additionally suggested by  
350 our finding that the larger the number of eggs in the clutch, the lower the blood THg concentrations.

351 Similar evidence of egg laying being an efficient route of mercury excretion for female terns is provided  
352 by studies showing that mercury deposition in eggs decreases across the laying sequence, likely due to  
353 a reduced ‘availability’ of mercury in females for excretion into subsequent eggs after the first one is  
354 laid (Becker et al., 1992; Akearok et al., 2010; Ackerman et al., 2016). Previous studies, however, also  
355 indicated that other factors may additionally contribute to sex-differences in THg contamination  
356 (Robinson et al., 2012; Hitchcock et al., 2019). In double-crested cormorants (*Phalacrocorax auritus*),  
357 females, for example, were shown to have greater capacity to demethylate mercury in the liver than  
358 males (Robinson et al., 2011). Additionally or alternatively, males and females may differ in their levels  
359 of mercury excretion (Braune and Gaskin, 1987b). Given that moult does not take place during the early  
360 breeding season, excretion through faeces seems the only potential pathway in this respect. We,  
361 however, deem this unlikely to be important in our case, because faecal mercury exists only in inorganic  
362 form (Morrissey et al., 2005), and the uptake of inorganic mercury is minimal. However, further studies  
363 should address the potential impact of excretion mechanisms on sex-specific blood THg levels, as well  
364 as the effects of mercury deposited in eggs for the offspring (Ackerman et al., 2020).

365 Older birds of both sexes had significantly higher THg levels in their blood compared to young  
366 birds. We found no evidence for selective (dis)appearance of either weakly or heavily contaminated  
367 individuals, and our longitudinal data suggest that the higher THg levels in older individuals result from  
368 within-individual THg accumulation with age, the shape and extent of which differed somewhat between  
369 the sexes. Specifically, within-individual THg concentrations of males exhibited significant decelerating  
370 accumulation, whereas in females there was a trend towards a lesser but linear within-individual  
371 increase. Again, the ability of females to excrete MeHg through egg laying could explain why we  
372 observe a weaker accumulation with age in females than in males. However, this does not explain the  
373 trend towards the non-linear component of the within-individual age effect differing between males and  
374 females, given that female terns of our population increase their clutch size as they grow older (Zhang  
375 et al., 2015) and therefore would, if anything, be expected to show a stronger deceleration with age than  
376 males. Sex-specificity of mercury uptake, via the use of differential foraging areas (Carravieri et al.,  
377 2014; Militão et al., 2023) or differential prey choice (De Felipe et al., 2019), which additionally might  
378 be age-specific, is an alternative explanation that deserves empirical attention.

379 As also alluded to above, birds possess mechanisms that should mitigate the MeHg  
380 concentrations in their bodies. It is well-established that a substantial portion of ingested MeHg is  
381 deposited in feathers (Braune and Gaskin, 1987a), a phenomenon that may explain why in some bird  
382 species, such as wandering albatrosses, adults, undergoing frequent moulting, exhibit lower, rather than  
383 higher THg levels in blood compared to immature birds undergoing sporadic moults (Tavares et al.,  
384 2013; Bustamante et al., 2016). Moreover, mercury that is not excreted, such as that ingested during  
385 non-moulting periods, is typically demethylated in the liver to inorganic mercury by binding with  
386 selenium at a high rate (e.g. Eagles-Smith et al., 2009b; Manceau et al., 2021). These highly efficient  
387 mechanisms could account for the absence of mercury accumulation in blood observed in previous (but  
388 cross-sectional) studies on birds (Thompson et al., 1993; Becker et al., 2002; Carravieri et al., 2014,  
389 2022; Tartu et al., 2015). In addition, they could explain the rather slow rate of accumulation found in  
390 this study, although the fact that accumulation still occurs suggests that these mechanisms are limited.

391 The difference in the average THg levels between young (first quartile of age,  $0.90 \mu\text{g}\cdot\text{g}^{-1}$  ww,  
392  $n = 318$ ) and old (fourth quartile of age,  $1.17 \mu\text{g}\cdot\text{g}^{-1}$  ww,  $n = 308$ ) birds equals 30%, which combined  
393 with a relatively low individual repeatability of 20% (i.e. total phenotypic variance explained by  
394 individual identity as a random effect in the model described in Table 2a), raises concerns about the  
395 suitability of blood from birds of unknown age as an accurate bioindicator of environmental mercury  
396 levels, at least for common terns. The influence of age on mercury levels might, however, be less  
397 pronounced in other study systems, especially when considering additional variables such as isotopic  
398 data (Polito et al., 2016; Renedo et al., 2018a, 2018b; Jouanneau et al., 2022), different foraging  
399 locations (e.g., Ackerman et al., 2016), or species preying at lower trophic levels (Ma et al., 2021) or  
400 having shorter lifespans (Hallinger et al., 2011). Assessing the generality of the age-specificity of blood  
401 mercury contamination we found therefore is important. Moreover, further studies are also needed to  
402 investigate the age-specificity of (maternal) mercury levels in other commonly used bioindicator tissues,  
403 such as feathers (Sun et al., 2020) or eggs (Evers et al., 2003; Goodale et al., 2008).

404 It is noteworthy that the THg values of all of our 1314 blood samples collected from 588  
405 individual common terns exceeded the toxicity thresholds at which adverse health effects have been  
406 observed, with 57% being at low ( $0.2 - 1.0 \mu\text{g}\cdot\text{g}^{-1}$  ww) and 43% being at moderate ( $1.0 - 3.0 \mu\text{g}\cdot\text{g}^{-1}$

407 ww) risk levels, following the toxicity benchmarks published by Ackerman *et al.* (2016). As an  
408 endocrine disruptor, MeHg has been reported to decrease breeding probability (Tartu *et al.*, 2013; Goutte  
409 *et al.*, 2015), to alter risk-taking (Kobiela *et al.*, 2015) or parental behaviour (Tartu *et al.*, 2015) and  
410 oxidative stress status (Costantini *et al.*, 2014; Eckbo *et al.*, 2019; Soldatini *et al.*, 2020). Such effects  
411 could potentially impair the ability to adapt to environmental changes (Jenssen, 2006; Grunst *et al.*,  
412 2023a) or to mount an effective immune response against disease (Hawley *et al.*, 2009; Lewis *et al.*,  
413 2013). Moreover, mercury has been associated with a reduced body condition (Amenlineau *et al.*, 2019;  
414 Eckbo *et al.*, 2019; but see Carravieri *et al.*, 2022), which can be particularly harmful for migratory birds  
415 (Seewagen, 2020) when their flight performance (Ma *et al.*, 2018a) or fat deposition and muscle  
416 development (Adams *et al.*, 2020) would be compromised.

417 Overall our study suggests that the risk of suffering from the detrimental effects of mercury  
418 pollution differs between the sexes and increases as adult birds age. Although we so far found no  
419 evidence of selective (dis)appearance and previous studies on adult seabirds in wild populations mostly  
420 also reported no direct correlation between survival and mercury contamination (Thompson *et al.*, 1991;  
421 Goutte *et al.*, 2015; Bustamante *et al.*, 2016; Pollet *et al.*, 2017; Amélineau *et al.*, 2019; Chastel *et al.*,  
422 2022; but see Calvert *et al.*, 2024), interactions between mercury pollution and other stressors may have  
423 synergistic effects (Costantini *et al.*, 2014; Grunst *et al.*, 2023b; Smith *et al.*, 2023) and further studies  
424 are needed to assess how mercury pollution interacts with such stressors and whether effects may be  
425 sex- and/or age-specific as well.

426

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433

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