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1 Blood mercury concentrations in four sympatric gull species from
2 South Western France: insights from stable isotopes and biologging

3

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25 **ABSTRACT**

26 Mercury (Hg) is a toxic trace element widely distributed in the environment, which
27 particularly accumulates in top predators, including seabirds. Among seabirds, large gulls
28 (*Larus sp*) are generalist feeders, foraging in both terrestrial and marine habitats, making
29 them relevant bioindicators of local coastal Hg contamination. In the present study, we
30 reported blood Hg concentrations in adults and chicks of four different gull species
31 breeding on the French Atlantic coast: the European herring gull (*Larus argentatus*), the
32 Lesser black-backed gull (*L. fuscus*), the Great black-backed gull (*L. marinus*) and the
33 Yellow-legged gull (*L. michahellis*). We also investigated the potential role of foraging
34 ecology in shaping Hg contamination across species, using the unique combination of three
35 dietary tracers (carbon, nitrogen and sulfur stable isotopes) and biologging (GPS tracking).
36 A high concentration of Hg was associated with high trophic position and a marine diet in
37 gulls, which was corroborated by birds' space use strategy during foraging trips. Adults of
38 all four species reached Hg concentrations above reported toxicity thresholds. Specifically,
39 adults of Great black-backed gulls had a high trophic marine specialized diet and
40 significantly higher Hg concentrations than the three other species. Blood Hg was 4 to 7
41 times higher in adults than in chicks, although chicks of all species received mainly marine
42 and high trophic position prey, which is expected to be the cause of blood Hg
43 concentrations of toxic concern. By using both stable isotopes and GPS tracking, the
44 present study provides compelling insights on the main feeding habits driving Hg
45 contamination in a seabird assemblage feeding in complex coastal environments.

46

47 Key words: Contaminant, Trace element, Seabird, Habitat, Movement ecology, Stable
48 isotopes

49 **INTRODUCTION**

50 Mercury (Hg) is a non-essential trace element released by both natural and
51 anthropogenic processes (Pirrone et al., 2010). Organic Hg (mostly methylmercury; MeHg)
52 is the main bioavailable and toxic form for living organisms (Díez, 2008; Thompson and
53 Furness, 1989). MeHg is incorporated in organisms mainly via ingestion of contaminated
54 food (Eagles-Smith et al., 2018). In birds, accumulation of MeHg has been associated with
55 a wide range of behavioral and physiological detrimental consequences, impacting
56 individual fitness, and ultimately, population dynamics (Tan et al., 2009; Whitney and
57 Cristol, 2017). Due to a relatively long biological half-life in tissues (Stickel et al., 1977),
58 Hg tends to bioaccumulate in organisms over time and biomagnify up trophic food webs,
59 leading long-lived top predators to exhibit elevated Hg concentrations (Atwell et al., 1998;
60 Cherel et al., 2018; Evers et al., 2005). In coastal environments, seabirds are therefore
61 considered as excellent sentinels of the local contamination (Burger and Gochfeld, 2004;
62 Furness and Camphuysen, 1997; Monteiro and Furness, 1995).

63 Seabirds show a large interspecific variation in foraging strategies (Ceia and
64 Ramos, 2015), leading to varied degrees of Hg exposure among species (Carravieri et al.,
65 2014b; Monteiro et al., 1998; Stewart et al., 1997). Large gulls of the *Larus* genus are
66 omnivorous and opportunistic feeders. *Larus* spp. are known to exploit both marine and
67 terrestrial habitats, and can scavenge from multiple anthropogenic sources including waste
68 dumps, landfill sites and fishing discards, as well as predated upon eggs or chicks
69 (Buckley, 1990; Mudge and Ferns, 1982; Ramos et al., 2009). Assessing Hg concentrations
70 in sympatric *Larus* species with differences in foraging ecology thus enables to have an
71 overview of the local environmental contamination, particularly in complex coastal

72 habitats (Binkowski et al., 2020). Additionally, in seabirds, individual variation in foraging
73 behavior appears to be highly prevalent, with individuals differing in their resource use,
74 habitat selection, and their fidelity to foraging sites (Ceia and Ramos, 2015; Phillips et al.,
75 2017). Such variation in foraging behavior may be consistent over time, and linked to
76 individuals' characteristics, such as their age or sex (Bolnick et al., 2003). As Hg exposure
77 largely varies with feeding strategies and habitat use, this variability shapes intraspecific
78 differences in Hg contamination (Bustamante et al., 2016; Ceia and Ramos, 2015; Stewart
79 et al., 1997), with consequences for individual fitness. Characterizing foraging ecology at
80 the individual level is therefore essential to understand patterns of Hg contamination within
81 and among species.

82 Tracking devices, including Global Positioning System (GPS) loggers, enable fine
83 scale monitoring of an animal's movements, which facilitates a direct characterization of
84 its habitat use (Burger and Shaffer, 2008). Furthermore, recently developed analytical tools
85 - including hidden Markov models (HMMs) - facilitate behavioral classification of GPS
86 tracking data (Langrock et al., 2012), enabling the identification of the precise locations
87 and habitats in which animals are foraging. The analysis of stable isotopes – used as a
88 proxy for the trophic niche (Newsome et al., 2007) – can also represent an effective tool to
89 define the foraging habitats (carbon: $\delta^{13}\text{C}$ and sulfur: $\delta^{34}\text{S}$) and trophic positions (nitrogen:
90 $\delta^{15}\text{N}$) of seabirds (Hobson et al., 1994; Kelly, 2000; Lott et al., 2003). A marine diet is
91 characterized by higher $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values, as opposed to lower levels indicating
92 terrestrial food intakes (Chisholm et al., 1982; Hobson, 1987; MacAvoy et al., 2000;
93 Schoeninger and DeNiro, 1984). More specifically, $\delta^{34}\text{S}$ is preferentially used to
94 differentiate marine vs terrestrial foraging habitats, since it does not present a stepwise

95 enrichment within the food chain, and therefore shows a greater discriminating power than
96 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Hobson, 1999; McCutchan Jr et al., 2003). This characteristic makes $\delta^{34}\text{S}$
97 particularly interesting to depict seabirds' use of coastal habitats. Therefore, the use of GPS
98 trackers combined with isotopic measurements enables a holistic overview of birds'
99 feeding strategies with respect to multiple available foraging habitats, as well as a high
100 discriminant power (Bracey et al., 2021; Caron-Beaudoin et al., 2013; Ceia et al., 2018;
101 Mendes et al., 2018).

102 In France, Hg contamination of seabirds has been largely documented in overseas
103 departments and territories (e.g. French Guiana, Sebastiano et al., 2016; 2017; Scattered
104 Islands, Kojadinovic et al. 2007a; Réunion Island, Kojadinovic et al. 2007b; 2007c) and
105 French Southern and Antarctic Territories (e.g., Blévin et al., 2013; Carravieri et al., 2014;
106 2016; Goutte et al., 2014a; 2014b; Tartu et al., 2014; 2015a). Although the coasts of
107 metropolitan France host large numbers of breeding seabirds (e.g., 174 000 pairs, Cadiou,
108 2011), data on Hg concentrations in seabird tissues are scarce and limited to chicks of four
109 gull species (*Larus argentatus*, *Larus fuscus*, *Larus marinus* and *Larus michahellis*) from
110 the Southern Bay of Biscay and the English Channel (Binkowski et al., 2020; Zorrozueta et
111 al., 2020). In these studies, high blood Hg concentrations were associated with a diet of
112 marine origin and of high trophic position. Yet, our knowledge on Hg concentrations in
113 other potentially contaminated areas remains very limited.

114 In the present study, we investigated Hg concentrations in adults and chicks of four
115 gull species from a South Western France colony: Herring gulls *Larus argentatus*
116 *argenteus*, Lesser black-backed gulls *L. fuscus graellsii*, Great black-backed gulls *L.*
117 *marinus* and Yellow-legged gulls *L. michahellis*. We were particularly interested to i)

118 describe Hg concentrations of the species during the breeding period; ii) identify the factors
119 driving inter- and intraspecific Hg variations among adults and chicks – in relation to their
120 different feeding habitats inferred from blood $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ stable isotopes, and in
121 relation to their individuals characteristics as age and sex; and iii) explore whether fine-
122 scale habitat partitioning using GPS tracking further elucidates the potential variation in
123 adult Hg contamination. Due to the known differences in foraging ecology among the four
124 species, as well as the individual differences within species, we expected a high inter- and
125 intraspecific variation in Hg concentrations. We further predicted that i) individuals feeding
126 at higher trophic positions (indicated by higher $\delta^{15}\text{N}$ values) or foraging in marine habitats
127 (indicated by both high $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values, as well as GPS tracking) would exhibit higher
128 Hg concentrations; and that ii) these patterns would persist both between and within
129 species.

130

131 **MATERIALS AND METHODS**

132 **Field methodology**

133 In the breeding seasons of 2016-2019, we sampled gulls breeding in “Lilleau des
134 Niges” National Nature reserve, Ile de Ré, South Western France (46°13'53" N, 1°30'22"
135 W; Figure 1): European herring gulls (EHG, approx. 400 pairs), Lesser black-backed gulls
136 (LBBG, approx. 400 pairs), Great black-backed gulls (GBBG, approx. 200 pairs), and
137 Yellow-legged gull (YLG, approx. 100 pairs). Adult birds were sampled in May ($n = 140$),
138 and chicks in July ($n = 107$). All individuals were captured and sampled only once over the
139 four years. Annual sample sizes for adults and chicks of each species can be found in the
140 Supporting Information (SI) Table S1. Adults incubating a full-size clutch (i.e. 2 to 3 eggs)

141 were caught on their nests, using a trap placed over the eggs. Chicks of approximately 1
142 month of age were caught by hand, within the colony. From an early age, gull chicks are
143 developed enough to explore their environment and do not stay in their nest, therefore we
144 were unable to assign relatedness among chicks and adults. Skull and tarsus were measured
145 using a caliper (± 0.1 mm). Wing length was also measured using a ruler (± 1 mm), and
146 birds were weighted using a Pesola spring balance (± 5 g). Blood samples (2 mL, <1 % of
147 the body mass of LBBG, the smallest species in this study) were taken from the brachial
148 vein of adults and chicks using heparinized syringes. Blood was transferred into a 2 mL
149 Eppendorf[®] tube and immediately stored in a cool box. At the end of each sampling day,
150 whole blood was centrifuged and red blood cells (hereafter “blood”) were stored at -20°C
151 until laboratory analyses. Blood samples were then used to measure Hg and stable isotopes
152 and for molecular sexing.

153

154 **Mercury analysis**

155 The analysis of total Hg in lyophilized blood was carried out using an Altec AMA
156 254 spectrophotometer following Bustamante et al. (2006). Each sample (mass: ~ 0.5 mg
157 dry weight, dw) was analysed twice and Hg concentrations were then averaged. For each
158 individual, the relative standard deviation was <10 %. Accuracy was checked at the
159 beginning and the end of each measurement session using a certified reference material
160 (2016-2018: DOLT-5 dogfish liver - Hg certified concentration (mean \pm SD): 0.44 ± 0.18
161 $\mu\text{g g}^{-1}$ dw; 2019: TORT-3 lobster hepatopancreas - Hg certified concentration: 0.29 ± 0.02
162 $\mu\text{g g}^{-1}$ dw; obtained from NRC, Canada). Recoveries were respectively 0.422 ± 0.005 and
163 $0.318 \pm 0.014 \mu\text{g g}^{-1}$ dw. Blanks were also run before and after each set of samples. The

164 limit of detection of the AMA was 0.1 ng. Hg concentrations are expressed as $\mu\text{g g}^{-1}$ dw.
165 In several bird species, MeHg represents most of the total Hg in blood (Renedo et al., 2018;
166 Rimmer et al., 2005). Chicks accumulate Hg from hatching, being fed by their parents from
167 local food items. For this reason, they are relevant bioindicators of the local environment
168 contamination (Binkowski et al., 2020; Blévin et al., 2013). By contrast to chicks, using
169 adult gulls as bioindicators of their local environment during breeding is still debated as
170 the half-life of Hg in avian tissues is 1~3 months, and contaminants acquired during
171 migration might still be present in blood (Bearhop et al., 2000; Monteiro and Furness, 2001;
172 Stickel et al., 1977). However, all species used in the present study were on the breeding
173 grounds more than 3 months before sampling, therefore blood Hg should mainly represent
174 local contamination.

175

176 **Stable isotope analysis**

177 Sub-samples of blood were weighed (mean \pm SD: 0.29 ± 0.06 mg dw for $\delta^{13}\text{C}$ and
178 $\delta^{15}\text{N}$; 0.71 ± 0.05 mg dw for $\delta^{34}\text{S}$) with a microbalance and then packed into tin containers
179 for combustion. Relative abundances of carbon, nitrogen and sulfur isotopes were
180 measured using a continuous flow mass spectrometer (Thermo Scientific Delta V
181 Advantage) coupled with an elemental analyzer (carbon and nitrogen: Thermo Scientific
182 Flash EA 1112; sulfur: Thermo Scientific Flash IRMS EA IsoLink). The delta (δ) notation
183 relative to Vienna PeeDee Belemnite, atmospheric N_2 and Vienna Cañon Diablo troilite
184 for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ respectively, was used to present isotopic results. Accuracy was
185 checked by replicate measurements of the internal laboratory standard, and analytical
186 precision was <0.10 ‰ for $\delta^{13}\text{C}$, <0.15 ‰ for $\delta^{15}\text{N}$ and <0.20 ‰ for $\delta^{34}\text{S}$ values. The stable

187 isotopes values were computed as $\delta X = \left[\left(\frac{R_{Sample}}{R_{Standard}} \right) - 1 \right] \times 1000$, where X stands for ^{13}C ,
188 ^{15}N or ^{34}S and R being the ratio $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$ or $^{34}\text{S}/^{32}\text{S}$. Turnover time for $\delta^{13}\text{C}$ and δ
189 ^{15}N in blood is 11~30 days (Barquete et al., 2013; Hobson and Clark, 1992; 1993), therefore
190 stable isotopes values are representative of the breeding period in adults.

191

192 **GPS tracking analysis**

193 A subset ($n = 43$) of the captured adults (18 EHG, 18 LBBG and 7 GBBG, see SI Table S1)
194 were equipped with GPS-UHF loggers (HARRIER, Ecotone[®]) in 2017 and 2018. Among
195 the 43 GPS equipped birds, 17 EHG, 18 LBBG and 6 GBBG were blood sampled and
196 included in Hg and stable isotopes analyses. The total mass of the logger and the harness
197 (used for attachment) weighted on average 13g (i.e. <2 % of the body mass of LBBG, the
198 smallest species in this study).

199 GPS loggers were set to record locations every 5 min. For each tracked individual,
200 locations were filtered to the period between the day after blood sampling to the last day
201 before either nest failure or egg hatching had been recorded (Figure 1 & SI Figure S1 &
202 Table S2). Foraging sites were identified from GPS tracks by assigning a behavioral state
203 to each location using Hidden Markov Models (hereafter “HMMs”, Franke et al. 2004)
204 fitted using the moveHMM R package (Michelot et al., 2016). Additional information on
205 the spatial data treatment and the behavioral classification can be found in the SI. The
206 habitat for each of these locations was assigned as either “pelagic”; “coastal” (i.e. lagoons,
207 estuaries, coastal salt marshes, intertidal flats), or “terrestrial” (all others) based on the
208 CORINE Land Cover dataset (CORINE Land Cover; Feranec et al. 2016). Ratios of pelagic
209 vs coastal and marine (i.e., pelagic and coastal) vs terrestrial habitats used by each

210 individual were then calculated.

211 For an overview of the feeding behaviors leading to the observed Hg concentrations
212 in the tracked species, we estimated birds' foraging site fidelity. As well as giving important
213 insight into the degree of specialization in birds' uses of foraging habitat, this measure of
214 site fidelity served to test whether individuals' foraging behavior in the period after blood
215 sampling was likely to be representative of their behavior prior to blood sampling (see SI).
216 Individual foraging site fidelity was assessed following the randomization procedure of
217 Harris et al. (2020). For each foraging site, the distance to a randomly selected site from
218 the same individual during another trip (within-individual comparison), as well as to a
219 randomly selected site from each other individual of the same species (between-individual
220 comparisons) was measured. The site fidelity index corresponds to the proportion of
221 between-individual sites that were farther from the focal site than the within-individual
222 site. This index is bounded between 0 and 1, with high values representing high site fidelity
223 (an individual forages more closely to its own foraging sites than to the sites of other
224 individuals), and low values representing low site fidelity (an individual forages more
225 closely to the foraging sites of other individuals than to its own foraging sites). Additional
226 information can be found in the SI.

227

228 **Molecular sexing**

229 All adults and chicks ($n = 247$) were sexed using blood samples by polymerase
230 chain reaction (PCR) amplification of parts of two highly conserved genes (CHD) of sex
231 chromosomes, following Fridolfsson and Ellegren (1999).

232

233 **Statistical analyses**

234 Statistical analyses were performed using R 4.0.0 (R Core Team, 2020). One YLG
235 chick was removed from the dataset due to outliers in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values. In all species,
236 adults had much higher Hg concentrations than chicks, and therefore chicks and adults
237 were treated separately.

238 Firstly, relationships between Hg concentrations and diet (inferred by stable isotope
239 values) were investigated. As $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ were positively correlated in adults
240 (Pearson correlation >0.70 , $p <0.001$ for all relationships) and partially correlated in chicks
241 (correlation: C-N = 0.72, $p <0.001$; S-C = -0.15; S-N = -0.18, both $p >0.05$), principal
242 components analyses (“FactoMineR” R package, version 2.3; Lê et al., 2008) were
243 performed on the three isotopes to reduce the number of explanatory variables. Principal
244 components (PCs) which explained more than 80 % of the total variance were retained. In
245 adults, principal components analysis reduced $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ to one PC (PC₁)
246 explaining 83.6 % of the variance and equally influenced by $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ (SI Figure
247 S2 & Table S3). High PC₁ scores reflected high $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$. In chicks, principal
248 components analyses reduced $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ to two PCs explaining 92.0 % of the
249 variance (SI Figure S2 & Table S3). High PC₁ scores indicated high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values,
250 and high PC₂ scores indicated high $\delta^{34}\text{S}$ values. The isotopic niches, which are essential
251 for an overview of each species’ local feeding habits, were investigated, and the foraging
252 ecology of each species were illustrated and described in the SI. Generalized least square
253 (GLS) models were then used to investigate the effects of the selected PCs on Hg (“nlme”
254 R package, version 3.1-151; Pinheiro et al., 2020). For that, using Hg as the response
255 variable, we included as explanatory covariates the selected PCs and the species. Year was

256 not included as a predictor in the models to improve statistical power, and also because
257 four years of sampling was insufficient to evaluate temporal trends in Hg concentration.
258 We used GLS models instead of linear models (LM) due to heteroscedasticity in Hg
259 concentrations among species (see SI for further information). For both adults and chicks,
260 after running GLS models, Tukey post-hoc pairwise comparison tests were performed to
261 quantify the differences in Hg concentrations among species (“emmeans” R package,
262 version 1.7.1-1; Lenth et al., 2021). Although performed on only three variables, PCA
263 enabled the inclusion of ecological information provided by the three stable isotopes rather
264 than exploring the effect of each stable isotopes in independent models (similar conclusions
265 were obtained using both methods, see SI)

266 Secondly, as Hg levels were found to be highly variable among species, we ran one
267 LM per species to investigate differences between the sexes. With Hg as the response
268 variable, we included the sex as an explanatory variable. This model was not fitted for
269 adults of YLG as only a single female was sampled. In previous studies, chick age has been
270 found to be a key predictors of Hg contamination, as blood Hg strongly fluctuates during
271 chick growth, reaching highest concentrations when feathers stop growing (Spalding et al.,
272 2000). Morphology is commonly used as a proxy of chick age, and we therefore also
273 included the skull length (head and bill) in the LMs for chicks as an additional explanatory
274 variable. Where Hg differed significantly between sexes, an additional LM was built to
275 investigate whether this was linked to sex differences in diet, with the selected PCs fitted
276 as the response and sex as an explanatory variable.

277 Finally, in GPS-tracked adults, the impact of the use of marine or terrestrial habitats
278 on Hg concentrations was investigated using a GLS model: Hg was fitted as the response

279 variable, and the proportional use of marine vs terrestrial habitat and species (to control for
280 the variation among species) were included as explanatory covariates. A similar model was
281 built to investigate the impact of the use of coastal or pelagic habitats on Hg concentrations,
282 including coastal vs pelagic habitats and species (to control for the variation among species)
283 as explanatory covariates. Before modelling, two individuals that were tracked but not
284 blood sampled were removed from the dataset.

285 For all models, a set of candidate models including all possible combinations of the
286 predictors, ranging from the full model (that includes each of the stated variables) to the
287 null model was built. In each case, the best candidate model – i.e., the one with the lowest
288 second-order Akaike’s Information Criterion value for small sample size (AICc;
289 “AICcmodavg” R package, version 2.2-2; Mazerolle, 2017), or the most parsimonious
290 model among those with a $\Delta AICc \leq 2$ – was retained for inference. Homogeneity and
291 normality of the residuals were visually checked using plots of residuals vs fitted values
292 and histograms of the residuals (Zuur et al., 2007). In post-hoc tests, an $\alpha < 0.05$ threshold
293 was used to assess the significance of the tests.

294

295 **RESULTS**

296 **Mercury in relation to feeding habits as inferred by stable isotopes**

297 In chicks, Hg concentrations ranged from $0.27 \mu\text{g g}^{-1} \text{ dw}$ in EHG to $3.86 \mu\text{g g}^{-1} \text{ dw}$
298 in GBBG (Table 1). Model selection indicated that PC_1 and species were significant
299 predictors of Hg concentrations, but not PC_2 (SI Table S4). Post-hoc comparison test
300 showed that GBBG had the highest Hg concentrations, followed by YLG that was not
301 significantly different from EHG and LBBG, but LBBG had lower Hg concentrations than

302 EHG (Tables 1 & 2, Figure 2). Chicks also exhibited a positive relationship between Hg
303 concentration and PC₁ (estimate ± SE = 0.09 ± 0.03, $t = 3.49$, $p < 0.001$; Table 2 & Figure
304 3). Sex was not retained as a significant predictor of Hg concentration for any species, but
305 skull size (as a proxy for chick age) was included in the best model for GBBG only (SI
306 Table S5), with Hg significantly increasing with skull size in this species ($F_{1, 26} = 6.51$, $p =$
307 0.017; estimate ± SE = 0.04 ± 0.02).

308 In adults, individual blood Hg concentrations ranged from 0.89 µg g⁻¹ dw in EHG
309 to 21.5 µg g⁻¹ dw in GBBG (Table 1). Model selection showed that PC₁ and species were
310 significant predictors of Hg concentrations in adult gulls (SI Table S4). Post-hoc
311 comparison test indicated that GBBG had the highest Hg concentrations, while lower
312 concentrations were found in YLG, LBBG and EHG (not significantly different among
313 them; Tables 1 & 2, Figure 2). Adults also showed a significant and positive association
314 between Hg concentration and PC₁ (estimate ± SE = 0.55 ± 0.06, $t = 9.25$, $p < 0.001$; Table
315 2 & Figure 3). Sex was retained for GBBG only (SI Table S5), with males having higher
316 Hg concentrations than females in adults of this species ($F_{1, 35} = 19.2$, $p < 0.001$; estimate ±
317 SE = 4.62 ± 1.05). However, sex was not retained as a significant predictor of stable
318 isotopes in GBBG (PC₁; SI Table S6).

319

320 **Mercury in relation to habitat use as inferred by GPS tracking**

321 From GPS tracked adults, a total of 1069 foraging trips from 43 individuals were
322 recorded (612 in EHG, 304 in LBBG and 154 in GBBG). The three tracked species showed
323 different patterns of habitat use: GBBG forage predominantly at sea and showed low inter-
324 individual variation (average use of marine habitats ± SD: 0.93 ± 0.05 %), while EHG (0.63

325 ± 0.23 %) and LBBG (0.78 ± 0.17 %) individuals were more spread on a gradient from
326 strictly terrestrial to strictly marine (Figure 1 & SI Figure S3). The use of marine habitats
327 in EHG and GBBG was mainly coastal (proportion of coastal habitats use \pm SD: $0.58 \pm$
328 0.25 and 0.90 ± 0.07 respectively), while LBBG used pelagic and coastal habitats
329 (proportion of coastal habitats use \pm SD: 0.23 ± 0.16 ; Figure 1 & SI Figure S3). Model
330 selection indicated that the proportional use of marine *vs* terrestrial habitats and the species
331 were significant predictors of Hg variations (SI Table S7), Hg concentrations increased
332 with the use of marine habitats in all three species (Estimate \pm SE = 2.59 ± 0.99 , $t = 2.62$,
333 $p = 0.01$; Figure 4). Conversely, the coastal *vs* pelagic gradient was not a significant
334 predictor of Hg variations in the three gull species. (Table S7). GBBG, EHG and LBBG
335 exhibited a relatively high fidelity to foraging sites (fidelity index \pm SD = 0.71 ± 0.18 ; 0.59
336 ± 0.13 and 0.72 ± 0.13 respectively).

337

338 **DISCUSSION**

339 Blood Hg concentrations of four sympatric gull species were investigated in
340 relation to their foraging ecology inferred from stable isotopes $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ blood
341 values in adults and chicks, and from GPS tracking of adult birds. High Hg concentrations
342 were related to stable isotopes values representative of a high trophic position food, mainly
343 of marine origin. Foraging movements tracked during breeding corroborated the
344 relationship between Hg and the birds' foraging strategies with relation to terrestrial *vs*
345 marine habitat use. All species showed foraging site fidelity, indicating a degree of
346 specialization in their use of foraging sites, and thus high potential for consistent individual
347 differences in contaminant level to emerge. This led some adult individuals to exceed

348 reported toxicity thresholds in all four species, particularly in GBBG, showing extremely
349 high levels of Hg. These findings are also concerning for chicks, which predominantly
350 receive marine food from their parents, and are therefore likely to accumulate high
351 concentrations of Hg. Together, these results support the use of sympatric species of gulls
352 as bioindicators of contamination in complex coastal habitats.

353

354 **Mercury concentrations**

355 LBBG and GBBG chicks had blood Hg concentrations similar to those from the
356 French coast of the English Channel, although EHG chicks had higher Hg concentrations,
357 even compared to the colonies from the Seine estuary, one of the most polluted rivers in
358 Europe (Binkowski et al., 2020; Cossa et al., 2002). Toxicological benchmarks are usually
359 assessed for adult birds, meaning that chicks Hg concentrations can only be compared to
360 published thresholds from adults with caution. However, much lower blood Hg
361 concentrations have been associated with an impaired physiological condition in LBBG
362 chicks (lower metabolism markers, increased oxidative stress and increased anaerobic
363 metabolism; Santos et al., 2020). In the present study, all four species showed similar Hg
364 levels between sexes, likely because sex difference in contaminant exposure is usually
365 visible later in life. However, in GBBG we detected increased levels of Hg with skull size
366 (a proxy of chick age), but this result was not found in other species. Blood Hg is known
367 to increase with the chicks age when most of the feathers have grown (Ackerman et al.,
368 2011). This relationship may be easier to detect in GBBG as they grow larger, thus their
369 among individual variation in size is higher than the other investigated species.

370 Hg concentrations in adults ranged from similar (EHG and LBBG) to much higher
371 (YLG and GBBG) than in gulls from the Baltic Sea including EHG and GBBG, or Brown
372 skuas (*Stercorarius antarcticus lonnbergi*) from three colonies of the Southern Ocean
373 (Mills et al., 2022; Szumiło-Pilarska et al., 2017). Notably, we found GBBG to have
374 average blood Hg concentrations similar to those of the Wandering albatross (*Diomedea*
375 *exulans*; Anderson et al., 2009), the highest trophic position seabird in the Southern Ocean
376 (Cherel et al., 2017) and one of the species with the highest known Hg levels worldwide
377 (Blévin et al., 2013; Carravieri et al., 2014a; 2014b; Cherel et al., 2018). Such Hg
378 concentrations are known to significantly impact reproduction, including breeding success
379 in various bird species (Goutte et al., 2015; Tartu et al., 2013; 2014; 2015b; Ackerman et
380 al., 2016). As no physiological endpoints were measured in the present study, it is not
381 possible to directly draw conclusions on the impact of Hg concentrations of this population.
382 Other factors may also contribute to a reduced toxicity of Hg. For instance, selenium –
383 which was not measured in the present study – is an essential trace element which may
384 protect birds against Hg toxicity (Dietz et al., 2000; Manceau et al., 2021). However, Hg is
385 known to affect almost all aspects of avian physiology and life history traits (Sebastiano et
386 al., 2022; Tartu et al., 2015a; Whitney and Cristol, 2017). We therefore emphasize further
387 work to investigate whether the reported high blood Hg concentrations are detrimental to
388 the different species of birds in the region. Similarly to what we observed in GBBG, higher
389 concentrations of Hg in males than in females were previously found in other bird species
390 (Ackerman et al., 2007; Burgess et al., 2005; La Sala et al., 2011). Interestingly, incubating
391 GBBGs males and females were not found to differ in terms of stable isotopes
392 concentration, suggesting diet is not the main driver of this difference. A possible

393 explanation may be represented by the fact that female gulls deposit Hg into their eggs
394 therefore lowering their circulating contaminants (Lewis et al., 1993).

395

396 **Mercury concentrations in relation to foraging ecology**

397 The positive relationship between blood Hg concentrations and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values
398 observed in gull chicks is in agreement with previous studies on the same four species in
399 the English Channel (Binkowski et al., 2020) and the southern Bay of Biscay (Zorrozueta et
400 al., 2020). However, blood $\delta^{34}\text{S}$ was not found to be an important driver of Hg
401 contamination at Ile de Ré, contrary to chicks in the English Channel (Binkowski et al.,
402 2020) and Spain (Ramos et al., 2013). In the present study, chick isotopic values were in
403 the highest range values of those of their parents for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$, meaning that they
404 predominantly received food at a higher trophic position and of marine origin. A diet shift
405 after hatching – reflecting different food requirement before and after hatching – has
406 previously been described in EHG and other species of gulls (Annett and Pierotti, 1989;
407 Bukacińska et al., 1996; Pierotti and Annett, 1987). This specialized chick diet of low
408 marine prey diversity, provided by the parents, may explain why the terrestrial vs marine
409 gradient is not a good predictor of Hg variations in chicks.

410 Isotopic data showed that, similarly to chicks, blood Hg contamination was higher in
411 adult gulls feeding on marine than terrestrial items. This is consistent with previous studies
412 investigating the relationship between Hg and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ in coastal seabirds and
413 their prey (Gongora et al., 2018; Peterson et al., 2017). These patterns likely reflect the
414 biomagnifying characteristics of Hg along food webs, with longer and more complex food
415 webs in the marine environment (Bełdowska and Falkowska, 2016; Morel et al., 1998), as

416 well as that MeHg is mainly produced in the ocean (Chen et al., 2008). Conversely, some
417 previous studies did not report such relationship in other aquatic birds (Einoder et al., 2018;
418 Soldatini et al., 2020), however, the association between Hg and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ is complex
419 and largely depends on the species or their environments. Different environments likely
420 differ in their $\delta^{15}\text{N}$ baseline (Elliott et al., 2021), thus precluding comparing directly
421 consumers' $\delta^{15}\text{N}$ values as reflecting their trophic position. This is likely the case of gulls
422 from Ile de Ré, meaning that any blood $\delta^{15}\text{N}$ difference at the species or individual level
423 must be interpreted with caution, especially if their $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values indicate foraging
424 in different habitats.

425 In the present study, EHG, LBBG and YLG showed important inter-individual
426 variations in blood $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values, that characterize populations of generalist
427 species made of specialist individuals (Jaeger et al., 2009). In contrast, GBBG exhibited
428 narrower ranges for all isotopic values, representative of a specialist species. GBBG's
429 isotopic values were in the highest range of those of the other gull species, that characterize
430 a diet based on marine items ($\delta^{34}\text{S}$: +15 to +19 ‰), whereas EHG, LBBG and YLG
431 individuals showed a diet of mixed terrestrial, intertidal and marine sources (Nehlich, 2015;
432 Rees et al., 1978). The very high Hg concentrations found in GBBG are therefore most
433 likely related to its marine diet. These isotopic results are supported by the analyses of
434 foraging trips in EHG, LBBG and GBBG, as the use of a marine habitats was related to
435 higher blood Hg concentrations. In other species of coastal gulls equipped with tracking
436 devices, including the American Herring gull (*Larus smithsonianus*) and the Western gull
437 (*Larus occidentalis*), a similar pattern was recently observed, with individuals mainly
438 foraging in marine environments exhibiting the highest Hg concentrations (Clatterbuck et

439 al., 2021; Thorne et al., 2021). EHG showed higher use of coastal foraging sites but similar
440 Hg concentrations compared to the more pelagic LBBG. The coastal specialists GBBG
441 also presented the highest Hg concentrations, further suggesting that “marine vs terrestrial”
442 may represent a better gradient than “coastal vs pelagic” to explain Hg variations in gull
443 species. As $\delta^{34}\text{S}$ highly discriminates between terrestrial and marine habitats (McCutchan
444 Jr et al., 2003), we further stress the importance of the use of $\delta^{34}\text{S}$ as relevant index of
445 foraging habitats.

446 Nevertheless, Figures 3 & 4 reveal a weaker relationship between blood Hg and PC_1 in
447 GBBGs. It was however not possible to include the interaction between PC_1 and species in
448 the models to study if this relationship was different among species, due to the relatively
449 different range in PC_1 and Hg values between GBBG and the other species. In chicks, the
450 additive effect of maternal Hg initially transferred in the egg may contribute to blur the
451 relationship in all species.

452 Surprisingly, the range of Hg concentrations seems to be inversely correlated to the
453 isotopic niche width in adults, i.e., with the foraging habitat diversity. In the specialist
454 GBBG, high fidelity to foraging sites may explain the high inter-individual variation in Hg
455 concentration despite a narrow isotopic niche, i.e., birds feeding on a similar trophic
456 position prey but specialized in areas of different contamination intensities (river estuarine,
457 salt-marshes, intertidal area, open sea,...; Mitchell and Gilmour, 2008), generating
458 individual variation in Hg exposure. EHG and LBBG also exhibited a relatively high
459 fidelity to foraging sites, but the lower range of Hg concentrations compared to GBBG
460 suggests that the foraging areas provided by movement analyses are important to
461 understand the sources of Hg in specialist species.

462

463 **CONCLUSION**

464 In the present study, we have highlighted the need to refine ecotoxicological studies
465 with stable isotope analyses, as the trophic position (using $\delta^{15}\text{N}$ as a proxy) and the feeding
466 habitat ($\delta^{34}\text{S}$) were important drivers of blood Hg contamination. We also point out that not
467 only the use of GPS data highly reflects the results on Hg concentrations and habitat
468 selection through isotopic analyses, but it may further provides fundamental insights on
469 inter-individual contamination through habitat fidelity. We argue for the concomitant use
470 of both GPS and the stable isotopes method to characterize the sources of contaminants in
471 seabirds.

472 Our results also call for a potential toxicological risk in both chicks and adults. As
473 chicks receive high trophic position prey of marine origin from their parents, such diet
474 could lead to Hg concentrations of concern during their development. In adults, GBBG
475 showed particularly high concentrations of Hg due to its almost exclusively marine food.
476 Nonetheless, several adults of all four species might be at risk as exceeded previously
477 reported Hg toxicity thresholds. It is therefore fundamental to further investigate the
478 potential detrimental effects of Hg exposure on physiological and life-history traits of the
479 studied species.

480

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495

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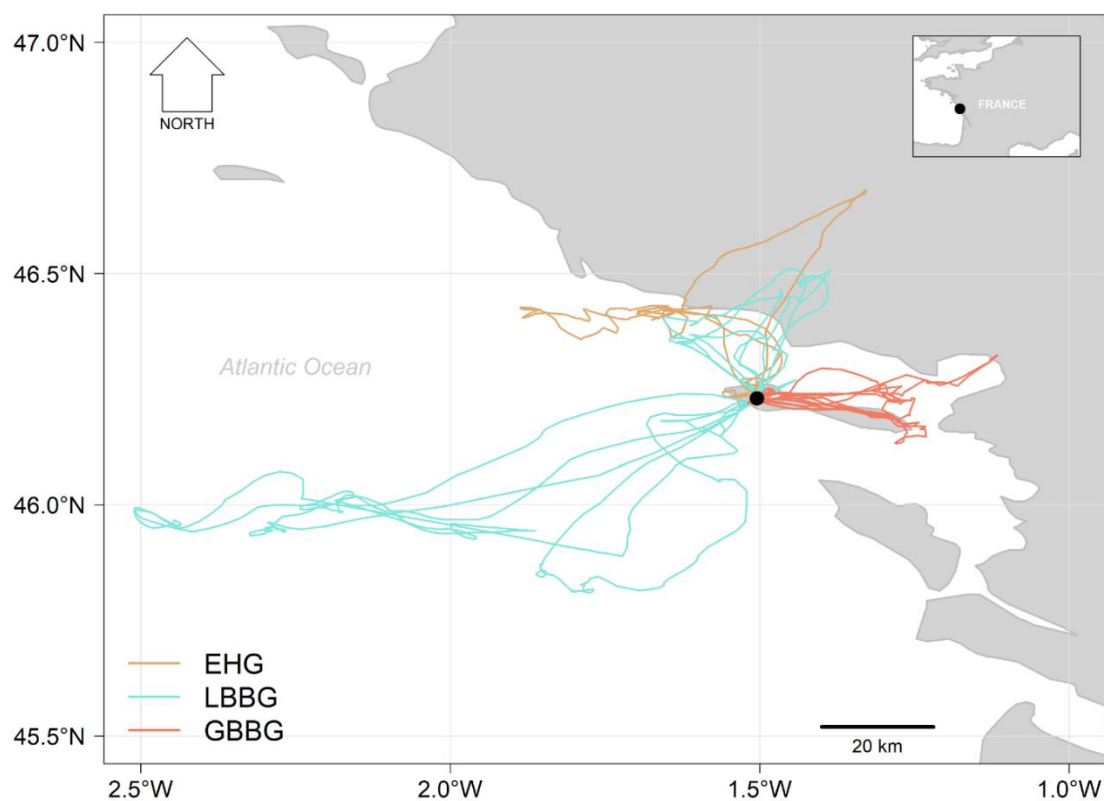
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502 **Figure 1.** Map of the Ile de Ré and surroundings, France, visited by the adults of four species of gulls from the “Lilleau des Niges”
503 colony during their breeding period; European herring gulls (EHG), Lesser black-backed gulls (LBBG), Great black-backed gulls
504 (GBBG) and Yellow-legged gulls (YLG). The studied colony is represented by the black point. YLG were not tracked and so are not
505 presented, but were included in analyses of Hg and stable isotopes. Tracks presented here are a random selection of 5 trips per species,
506 see SI Figure S1 for maps of all tracks per species.



507 **Table 1.** Hg concentrations ($\mu\text{g g}^{-1}$ dw) and carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulfur ($\delta^{34}\text{S}$) stable isotope values (‰) measured in blood
508 of adults and chicks of four gull species from the Ile de Ré, France: sample size (n), mean \pm standard deviation (SD), median and range
509 (min-max). For adults, Hg values are presented separately for females (♀) and males (♂).

		Adults							
		Hg		$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		$\delta^{34}\text{S}$	
	n	Mean \pm SD	Min/max	Mean \pm SD	Min/max	Mean \pm SD	Min/max	Mean \pm SD	Min/max
EHG (<i>Larus argentatus</i>)	44	2.29 \pm 1.06	0.89/5.01	-19.4 \pm 1.93	-22.9/-15.5	12.7 \pm 1.82	9.76/16.0	13.1 \pm 2.23	8.72/17.0
♀	23	2.05 \pm 0.96	0.90/4.31						
♂	21	2.55 \pm 1.12	0.89/5.01						
LBBG (<i>Larus fuscus</i>)	54	3.08 \pm 1.31	0.95/6.42	-19.1 \pm 1.34	-22.6/-17.6	13.8 \pm 1.30	10.9/15.8	15.9 \pm 2.37	9.90/18.6
♀	27	2.82 \pm 1.03	0.98/4.78						
♂	27	3.35 \pm 1.52	0.95/6.42						
GBBG (<i>Larus marinus</i>)	37	12.5 \pm 3.93	6.97/21.5	-16.8 \pm 0.83	-19.7/-14.7	16.4 \pm 0.41	15.8/17.8	16.9 \pm 1.07	14.6/18.7
♀	19	10.3 \pm 2.20	6.97/13.8						
♂	18	14.9 \pm 4.00	7.26/21.5						
YLG (<i>Larus michahellis</i>)	5	6.00 \pm 2.72	2.25/9.63	-19.4 \pm 3.51	-25.2/-16.7	15.1 \pm 1.32	12.76/15.91	12.6 \pm 4.66	5.87/16.7
♀	1	2.25 \pm NA	2.25/2.25						
♂	4	6.94 \pm 2.00	5.26/9.63						
		Chicks							
		Hg		$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		$\delta^{34}\text{S}$	
	n	Mean \pm SD	Min/max	Mean \pm SD	Min/max	Mean \pm SD	Min/max	Mean \pm SD	Min/max
EHG (<i>Larus argentatus</i>)	30	0.68 \pm 0.25	0.27/1.19	-18.3 \pm 0.66	-19.9/-17.1	13.8 \pm 0.75	12.1/15.0	16.8 \pm 1.21	14.0/18.7
LBBG (<i>Larus fuscus</i>)	37	0.58 \pm 0.15	0.35/0.94	-18.3 \pm 0.27	-18.8/-17.7	14.5 \pm 0.41	13.7/15.2	18.4 \pm 0.93	16.7/19.8
GBBG (<i>Larus marinus</i>)	28	1.91 \pm 0.76	0.81/3.86	-17.1 \pm 0.77	-19.33/-16.7	15.6 \pm 0.48	14.0/16.6	16.5 \pm 1.32	12.8/18.6
YLG (<i>Larus michahellis</i>)	11	0.90 \pm 0.34	0.48/1.75	-18.0 \pm 0.61	-19.37/-17.42	14.9 \pm 1.07	12.4/16.1	16.5 \pm 1.46	14.07/18.4

510

511 **Table 2.** Outputs of linear models examining the variables affecting Hg concentration in
 512 four gull species from the Ile de Ré, France: European herring gulls (EHG), Lesser black-
 513 backed gulls (LBBG), Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG).
 514 Significant *p*-values are in bold.

515

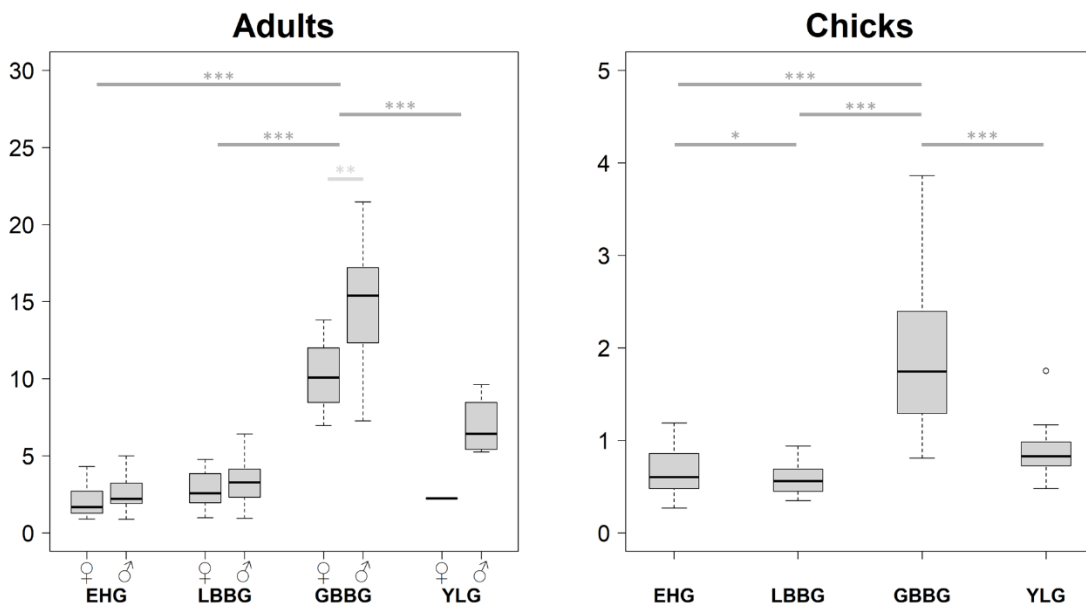
Adults				
Parameter	Estimate	SE	<i>t</i>-value	<i>p</i>-value
PC ₁	0.55	0.06	9.25	<0.001
EHG - LBBG	0.10	0.19	0.56	0.943
EHG - GBBG	8.56	0.67	12.70	<0.001
EHG - YLG	2.65	0.79	3.38	0.089
LBBG - GBBG	8.45	0.66	12.79	<0.001
LBBG - YLG	2.55	0.79	3.22	0.099
GBBG - YLG	-5.90	1.02	-5.78	<0.001

516

Chicks				
Parameter	Estimate	SE	<i>t</i>-value	<i>p</i>-value
PC ₁	0.09	0.03	3.49	<0.001
EHG - LBBG	-0.13	0.05	-2.72	0.043
EHG - GBBG	1.01	0.16	6.33	<0.001
EHG - YLG	0.11	0.12	0.93	0.792
LBBG - GBBG	1.14	0.15	7.45	<0.001
LBBG - YLG	0.24	0.11	2.16	0.189
GBBG - YLG	-0.90	0.18	-5.05	<0.001

517

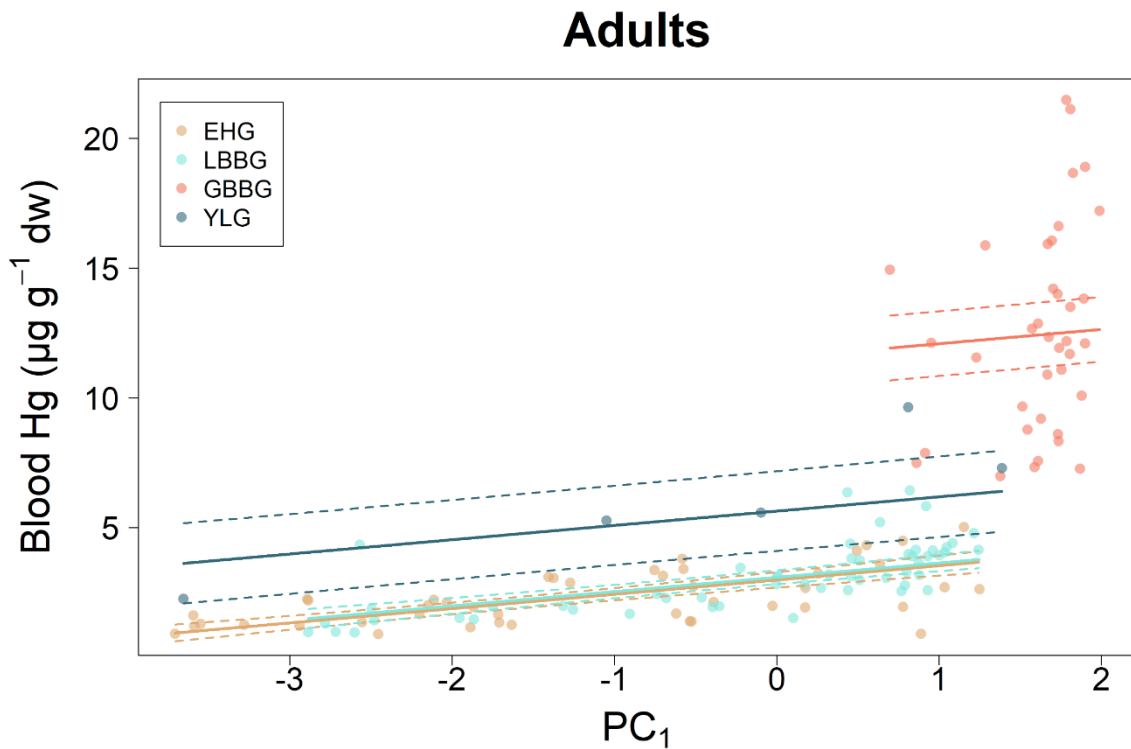
518 **Figure 2.** Blood concentrations of Hg in adults and chicks of four gull species from the
 519 Ile de Ré, France; European herring gulls (EHG), Lesser black-backed gulls (LBBG),
 520 Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG). For adults (left), Hg
 521 values are shown separately for females (♀) and males (♂). Interspecific (dark-grey) and
 522 between sex (light grey) statistically significant differences are indicated by the asterisk:
 523 *, **, ***; indicating a *p*-value < 0.05, <0.01, and <0.001, respectively. Values are
 524 median, 25th and 75th percentiles and range.
 525



526 **Figure 3.** Relationship between blood Hg concentrations and PC₁ ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$
527 values in adults and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ in chicks) or PC₂ ($\delta^{34}\text{S}$ values in chicks) of four gull species
528 from Ile de Ré, France: European herring gulls (EHG), Lesser black-backed gulls (LBBG),
529 Great black-backed gulls (GBBG) and Yellow-legged gulls (YLG). For each species, the
530 solid line refers to the fitted models obtained and dotted lines represent 95 % confident
531 intervals.

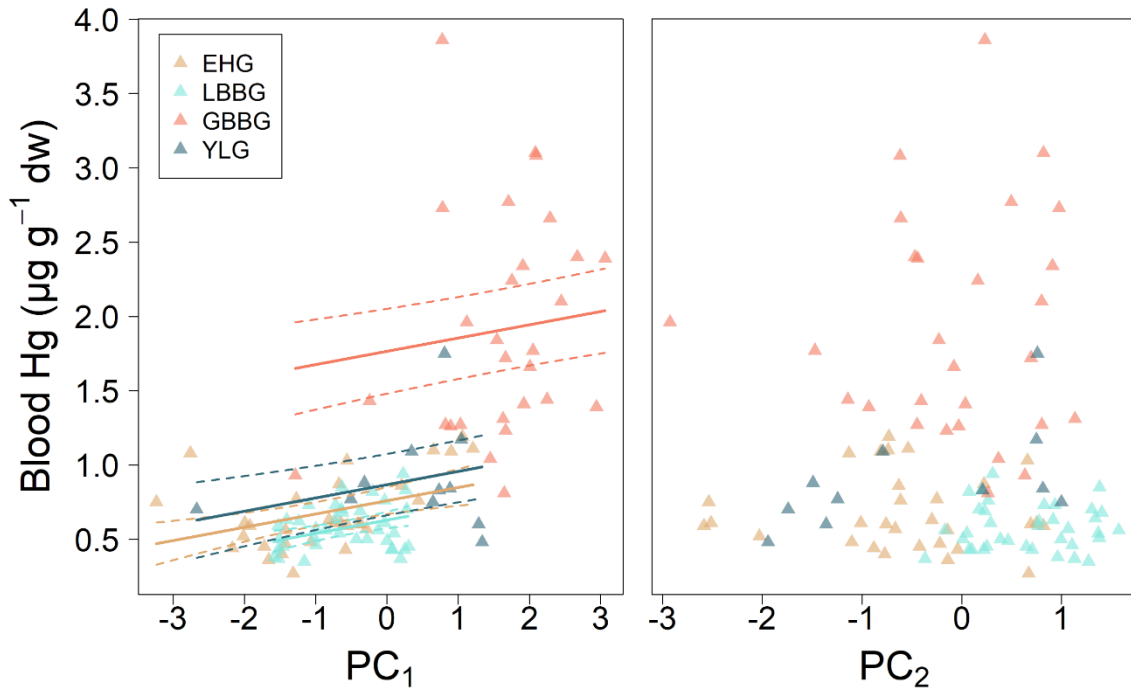
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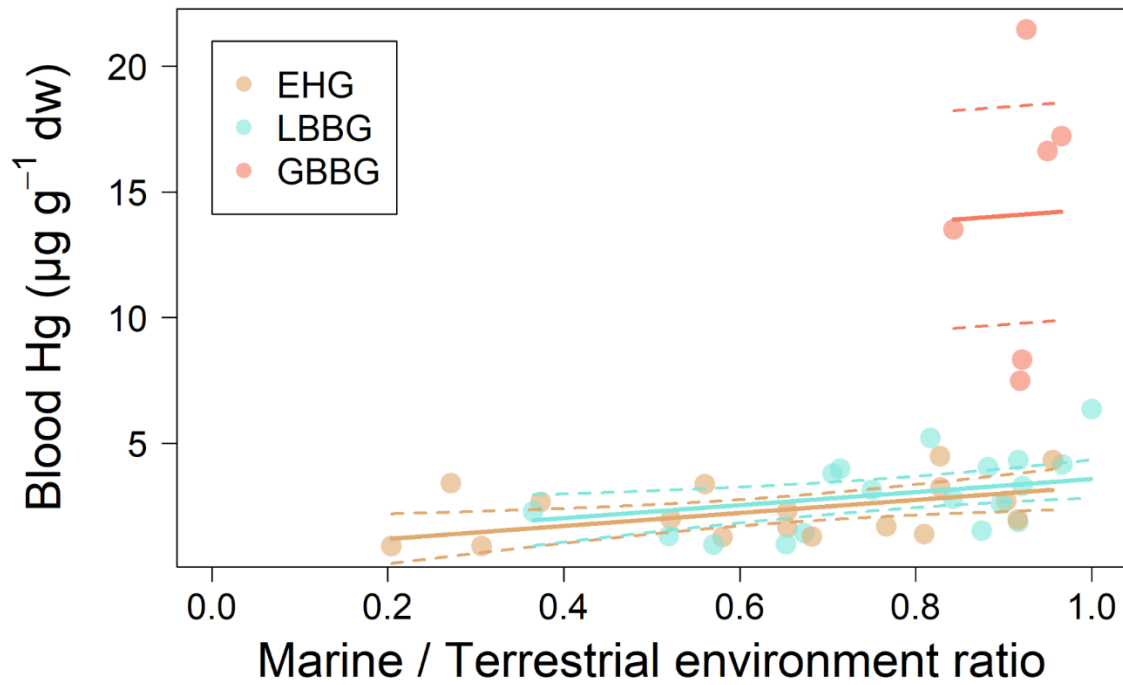
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Chicks



535

536 **Figure 4.** Relationship between blood Hg concentrations and the proportion of foraging
537 trips in marine (1: exclusively marine) vs terrestrial (0: exclusively terrestrial) habitats
538 obtain by GPS tracking in adults of three gull species from Ile de Ré, France; European
539 herring gulls (EHG), Lesser black-backed gulls (LBBG) and Great black-backed gulls
540 (GBBG). For each species, the solid line refers to the fitted models obtained and dotted
541 lines represent 95 % confident intervals.
542



543

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