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1       **Mercury concentrations in blood and back feathers are repeatable, heritable and**  
2                                       **correlated in a long-lived seabird**

3

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20       mercury tolerance, seabird

21 **ABSTRACT**

22 Mercury pollution is increasing both in the environment and in various organisms, especially  
23 top-predators. If variation in individual mercury concentrations is underpinned by genetic  
24 among-individual differences in traits related to mercury uptake, storage or excretion, and  
25 results in variation in fitness, populations may have the potential to evolve in response to this  
26 development. Few studies, however, have been able to collect sufficient information to  
27 investigate the genetic basis of pollution levels. We ran Bayesian quantitative genetic analyses,  
28 combining pedigree information obtained from a marine top-predator, the common tern (*Sterna*  
29 *hirundo*), with total mercury concentrations (THg) measured in 1364 blood and 1560 back  
30 feather samples obtained from >600 individual birds across seven years. Blood and back feather  
31 THg concentrations differed in repeatability (19 vs. 64%, respectively), but showed similar  
32 levels of heritability (c. 9%) and evolvability (c. 2%). Blood and back feather THg  
33 concentrations were positively correlated at the phenotypic, but not genetic, level. Although  
34 further work is needed to elucidate the uptake, storage or excretion pathways underlying these  
35 patterns, our study provides pioneering insights into the architecture of THg concentrations,  
36 and suggests that adaptation to environmental pollution may to some extent be possible.

## 37 INTRODUCTION

38 Mercury is a toxic trace element, the environmental presence of which has increased  
39 dramatically over the last 100 years due to human activities and is expected to continue to  
40 increase as global warming progresses (UN Environment, 2019). When it enters aquatic  
41 environments, mercury is methylated by microorganisms to its most toxic and bioavailable  
42 form, methylmercury (MeHg; Driscoll et al., 2013). Once in the food chain, MeHg accumulates  
43 both across (Atwell et al., 1998) and within (Bertram et al., 2024) organisms, making long-lived  
44 top-predators, such as various seabirds, particularly vulnerable to its detrimental effects. These  
45 detrimental effects include declines in health parameters, as well as impairment of fitness  
46 components. Reproductive performance, for example, can be reduced by mercury  
47 contamination, either indirectly through endocrine disruption (Tartu et al., 2015), or directly  
48 through embryo toxicity (Heinz and Hoffmann, 2003; Herring et al., 2010), or reduced offspring  
49 development (Amélineau et al., 2019) and survival (Goutte et al., 2014; Whitney and Cristol,  
50 2017).

51 While it is obvious that the levels of mercury present in an individual will to a large  
52 extent be driven by general environmental factors (e.g., the extent of contamination of foraging  
53 and breeding areas, Tartu et al., 2022), variation among individuals within populations is known  
54 to exist. Such variation can be underpinned by variation in intrinsic factors such as sex and age  
55 (Bertram et al., 2024), which themselves may be caused or supplemented by individual  
56 variation in the uptake of mercury from the environment, for example due to consistent  
57 differences in diet (e.g., Binkowski et al., 2020), or in the storage or excretion of mercury, for  
58 example due to consistent differences in metabolic rate (Gerson et al., 2019) or demethylation  
59 capacities in the liver (Eagles-Smith et al., 2009). If such differences are consistent due to being  
60 underpinned by a genetic basis, then the combination of genetic variation in traits linked to  
61 mercury contamination levels, and birds with lower levels of mercury contamination having a

62 selective advantage over their conspecifics, may lead to micro-evolution of these traits and to  
63 some extent facilitate adaptation to changes in environmental pollution levels.

64 Phenotypic variation in wild populations is generally the result of many genes with small  
65 effects (additive genetic variance), that often act in combination with individual variation  
66 introduced during development (permanent individual variance), and environmental effects  
67 such as abiotic or biotic factors (environmental variance). Quantitative genetics, as a field, aims  
68 at understanding the phenotypic diversity among individuals within a single population, and the  
69 extent to which this diversity stems from genetic and non-genetic causes, hence investigating  
70 the relative contribution of ‘nature’ vs ‘nurture’ to phenotypic variation (Falconer and Mackay,  
71 1996). By applying a statistical model based on a variance-partitioning approach, quantitative  
72 genetics allows the estimation of traits’ heritability, i.e., the relative contribution of additive  
73 genetic variance to the total phenotypic variation across individuals. In addition to the  
74 heritability, quantitative genetic analyses allow to estimate the correlation structure between  
75 heritable traits (Falconer and Mackay, 1996).

76 Despite extensive work documenting multiple aspects of mercury contamination across  
77 a wide taxonomic range (e.g., Wolfe et al., 1998; Scheuhammer et al., 2007; Dietz et al., 2021),  
78 we are aware of only two studies that have assessed the heritability of mercury-related traits in  
79 birds (Varian-Ramos et al., 2014; Buck et al., 2016). A study on captive zebra finches  
80 (*Taeniopygia guttata*, Varian-Ramos et al., 2014) found the reproductive success of individuals  
81 fed with a high mercury diet to be less compromised in the second generation (i.e., individuals  
82 exposed to mercury throughout their entire lives) than in the first generation (i.e., individuals  
83 exposed to mercury as adults only), despite blood mercury levels being very similar in both  
84 generations. This change across generations seemed consistent with patterns of rapid adaptation  
85 to mercury exposure, and hence, provided indirect evidence for a heritable basis of a tolerance  
86 trait (Varian-Ramos et al., 2014). In a follow-up study, Buck et al. (2016) found that zebra  
87 finches fed with a low or high dose of mercury showed no clear additive genetic variation in

88 mercury accumulation, while individuals exposed to intermediate dietary mercury did display  
89 a significant heritability. This non-linear genetic influence on blood mercury was attributed to  
90 the high energetic cost of adaptation outweighing the benefits of tolerance, at least in the  
91 treatment with low mercury contamination.

92         To assess whether susceptibility to mercury contamination is also heritable in wild  
93 populations, we used a quantitative genetics framework and combined phenotypic data on  
94 mercury concentrations with information on relatedness in a long-lived marine top-predator.  
95 Specifically, we quantified total mercury concentrations (THg) in 1364 blood samples and 1560  
96 back feather samples collected from >600 common terns (*Sterna hirundo*) at their breeding  
97 colony at the North Sea coast of Germany. Our study had two main objectives. First, we  
98 quantified the total phenotypic variation in THg explained by differences among individuals  
99 and by the additive genetic component in both traits (i.e., repeatability and heritability,  
100 respectively), as well as their evolvability (i.e., the additive genetic variance standardized by  
101 the trait's mean, quantified as the coefficient of additive genetic variation, Houle, 1992; Hansen  
102 et al., 2011). Second, we investigated whether blood and back feather THg were correlated at  
103 different levels of hierarchical variation. If individual blood and back feather THg harbour  
104 important, and independent or positively correlated, additive genetic variation, then the traits  
105 have the potential to evolve in response to natural selection, opening up largely unexplored  
106 avenues for wild populations to adapt to environmental pollution. For the data analyses, we  
107 implemented a Bayesian statistical framework using the R-package MCMCglmm (Hadfield,  
108 2010). Bayesian statistical analyses are commonly used in studies of quantitative genetics  
109 (Sorensen et al., 2002), because, among other reasons, the use of Markov Chain Monte Carlo  
110 (MCMC) readily allows to obtain the full posterior distribution of model estimates, facilitating  
111 the calculation of derived parameters with their associated uncertainty, such as the heritability  
112 (Sorensen et al., 1994; Sorensen et al., 2002).

113

## 114 **METHODS**

### 115 **STUDY SPECIES AND DATA COLLECTION**

116 We studied mercury contamination in piscivorous, migratory common terns breeding at a  
117 monospecific colony located at the Banter See in Wilhelmshaven at the German North Sea coast  
118 (53°30'40" N, 08°06'20" E). Previous studies have indicated that mercury contamination in the  
119 birds of this colony is particularly high (Bertram et al., 2024), which may be due to an increase  
120 in mercury concentrations in local fish populations over time (Kammann et al., 2023). Birds  
121 from the studied population overwinter along the African south- and west coast and show a  
122 high level of site-fidelity both to their wintering (Kürten et al., 2022) and breeding areas  
123 (Szostek and Becker, 2012). At an average age of three, they start their first breeding attempt  
124 and remain largely faithful to their breeding partners, with which they share incubation of the  
125 one to three eggs as well as chick rearing (Becker and Ludwigs, 2004). Since 1992, each nest  
126 at the Banter See colony is monitored three times weekly, and all locally hatched chicks are  
127 marked with rings just after hatching, as well as with subcutaneously-implanted transponders  
128 just prior to fledging (Becker and Wendeln, 1997). Their sex is determined molecularly  
129 following Becker and Wink (2003). Breeding adults are identified using portable antennae  
130 placed around each nest for 1–2 days during incubation.

131 Samples were collected between mid-May and early August 2017–2023. To collect  
132 blood samples, we used Mexican kissing bugs (*Dipetalogaster maxima*). One or two starved  
133 bugs, laboratory-bred for this purpose, were inserted into a hollow artificial egg and placed in  
134 the nest of a focal bird. Through small holes in the artificial egg, bugs were able to suck the  
135 birds' blood for c. 20 – 30 minutes, after which we extracted it from their abdomen with a  
136 syringe (following Becker et al., 2006) and stored it at -18°C until analysis. We corroborated  
137 that our sampling approach using bugs, in particular the bugs' physiology, had no impact on  
138 the measured THg concentrations by additionally blood sampling 18 birds from the branchial  
139 vein (correlation of 93%, Bertram et al., 2024). As part of a project involving the tracking of

140 common terns to their wintering areas, birds were caught with an electronically released drop  
141 trap (see Kürten et al., 2022). While the birds were being handled, five to ten feathers were  
142 collected from their backs (Bertram et al., 2022). These back feathers are among the first to  
143 grow at the onset of prenuptial moult, just before spring migration (Dwight, 1901). The  
144 individual repeatability of mercury concentrations in these back feathers within the same year  
145 was previously evaluated by analysing 3 – 6 feathers from the same bird year across three  
146 measurement batches (i.e., with 1 – 2 feathers per batch), resulting in three mercury  
147 concentrations for back feathers for each sample (bird per year). The repeatability of these three  
148 measurements was  $0.75 \pm 0.03$  SE (Bertram et al., 2022).

149         Using the nest-level information of incubating adults and their offspring, we constructed  
150 a social pedigree. This pedigree is a good approximation of the genetic pedigree, because  
151 common terns exhibit very low levels of extra-pair paternity (González-Solís et al., 2001). The  
152 pedigree was constructed by assigning all fledged offspring to their social parents and then  
153 pruned to remove individuals who were either not phenotyped or not ancestors to phenotyped  
154 individuals. In this study, the pruned pedigree had a maximum depth of five generations, and  
155 comprised 971 and 564 records for blood and back feather samples, respectively. The numbers  
156 of paternities and maternities were 386 for blood samples, and 238 paternities and 228  
157 maternities for back feather samples.

158

## 159 **MERCURY ANALYSIS**

160 Mercury analysis was performed using a Direct Mercury Analyzer (DMA-80, MLS  
161 Mikrowellen-Labor-Systeme GmbH, Germany). To remove potential external contamination,  
162 back feathers were alternately washed three times with distilled water and acetone, before being  
163 cleaned in an ultrasonic bath (Sonorex Super RK510H, Bandelin, Germany) after each wash  
164 for 15 min. Blood samples required no further preparation prior to analysis, i.e. were not dried.  
165 To determine the THg concentrations in the samples (in dry weight (dw) for back feathers, and



166 in wet weight (ww) for blood), 1–2 back feathers were wrapped in mercury free aluminium  
167 foil, or 20 µl of whole blood was loaded into a nickel sample boat and weighed. These samples  
168 were then introduced into the DMA-80 and burned at 750°C. During this process, gaseous  
169 mercury was released and trapped in the amalgamator as gold amalgamation, preserving the  
170 mercury from being burned with the other compounds of the sample. Subsequent heating to  
171 850°C released the mercury, enabling its quantification using atomic absorption spectrometry  
172 at 253.7 nm. In each measurement batch, we included an analytical blank to confirm the absence  
173 of device contamination, and a certified reference material (DORM-4; fish protein from  
174 National Research Council, Canada, 412 µg·kg<sup>-1</sup> dry weight; with a mean percent recovery ±  
175 standard deviation of 103 ± 9%). As part of the laboratory's quality assurance and quality  
176 control (QA/QC) measures, it participates biannually in the QUASIMEME international  
177 laboratory performance study program, consistently achieving satisfactory results. To further  
178 ensure the robustness of our analyses and subsequent conclusions related to back feather THg  
179 data, we collected three back feather samples of an individual in each sampling event, and found  
180 a high repeatability of back feather THg among them (75%, also see above; Bertram et al.,  
181 2022). To ensure the robustness of our study in terms of blood THg data, we blindly measured  
182 77 blood samples in duplicate and found a relative difference of 10 ± 11 % and a strong and  
183 significant correlation of 88% among the two measurements (Bertram et al., 2024).

184 In total, our dataset of THg concentrations in blood comprised 1364 observations from  
185 645 individuals, with a mean number of observations per individual of 2.11 (range 1 – 7). Our  
186 dataset of THg concentrations in back feathers comprised 1560 observations from 316  
187 individuals with a mean number of observations per individual of 4.93 (range 3 – 18, with three  
188 observations for each bird within a sampling event).

189

## 190 **STATISTICAL ANALYSES**

### 191 **Sources of variation in THg concentrations in blood and back feather samples**

192 We made use of a particular type of mixed-effects model known as the “animal model” (Lynch  
193 and Walsh, 1998; Kruuk, 2004). Animal models readily allow to estimate parameters such as  
194 the additive genetic variance and heritability by incorporating the population pedigree matrix  
195 as a random effect in the model. The model integrates information from the same individual  
196 identity in the mercury dataset and in the pedigree matrix, and hence is able to assess to which  
197 extent the genetic relatedness among individuals, extracted from the multigenerational  
198 pedigree, explains similarity in their (mercury) phenotypes, while also correcting for other  
199 sources of variation, such as permanent environment effects (see below).

200         Specifically, to investigate the sources of variation that underpin phenotypic differences  
201 in THg concentrations, we built two of such mixed-effects “animal models” (Kruuk, 2004)  
202 where THg concentrations in blood or in back feathers were the response variables,  
203 respectively. Both variables were log-transformed and we assumed Gaussian error  
204 distributions. As fixed effects in both models, we included the linear and quadratic effects of  
205 age (continuous variable measured in years, ranging from two to 27 years), as well as sex  
206 (categorical variable with two levels: male or female). As a random effect in both models, we  
207 included intercepts for individual identity linked to the multigenerational pedigree matrix  
208 constructed with information on the known relatedness of individuals in the population,  
209 allowing us to estimate the additive genetic variance. We also included intercepts for individual  
210 identity, but in this case not linked to the pedigree, to account for repeated measures within the  
211 same individual. This effect is commonly defined as the “permanent environment” effect  
212 (Lynch and Walsh, 1998; Kruuk, 2004), and encapsulates variance from developmental  
213 environment effects and/or non-additive genetic effects. Finally, we fitted intercepts for year of  
214 sampling to control for variation among years. In the model of THg concentrations in back  
215 feathers, we also fitted a composite variable grouping individual identity and year, to account  
216 for repeated measures of the same individual within a year. Repeatabilities (R) and heritabilities  
217 ( $h^2$ ), conditional to the variance explained by the fixed effects, were estimated as the proportion

218 of the total phenotypic variance explained by the individual variance and by the additive genetic  
219 variance, respectively. Evolvabilities were estimated as the coefficients of additive genetic  
220 variance ( $CV_A$ , Houle, 1992; Hansen et al., 2011)

221

## 222 **Correlations between THg concentrations in blood and back feather samples**

223 Our dataset contained 1155 measurements from 194 individuals for whom we had data on THg  
224 concentrations from both tissue types. We fitted a bivariate “animal model” to investigate  
225 whether these concentrations covaried, and at which level (i.e., genetic, individual and/or year).  
226 To do so, we simultaneously modelled both THg concentrations as response variables assuming  
227 a Gaussian error distribution, and fitted the same fixed and random effects as for the univariate  
228 models (Table 1). Additionally, we modelled an unstructured (co)variance matrix for additive  
229 genetic, individual (permanent environmental) and year variance components. Residual  
230 covariance was not fitted because measurements of THg concentrations were taken repeatedly,  
231 but at different times. We obtained correlations by dividing the covariance of two THg measures  
232 by the product of their variances.

233

## 234 **Statistical model implementation**

235 All models were fitted using a Bayesian framework implemented in the statistical software R  
236 (v. 4.3.0, R Core Team 2023) using the R-package *MCMCglmm* (Hadfield, 2010). For all  
237 models, we used inverse-gamma priors. The number of iterations and thinning intervals were  
238 chosen to ensure that the minimum MCMC effective sample size for all parameters was 1000.  
239 Burn-in was set to a minimum of 2000 iterations. The retained effective sample sizes yielded  
240 absolute autocorrelation values  $<0.1$  and satisfied convergence criteria based on the  
241 Heidelberger and Welch convergence diagnostic (Heidelberger and Welch, 1981). We drew  
242 inferences from posterior modes, posterior medians and 95% Credible Intervals (95% CI).

243

## 244 RESULTS

245 The overall mean ( $\pm$  SE) THg concentrations across the seven years of data included in our  
246 study were  $1.00 \pm 0.38 \mu\text{g}\cdot\text{g}^{-1}$  wet weight in blood, and  $3.48 \pm 2.32 \mu\text{g}\cdot\text{g}^{-1}$  dry weight in back  
247 feathers. Confirming previous work using a subset of these data (Bertram et al., 2024), THg  
248 concentrations in blood were higher in males than in females, and increased with age in a  
249 decelerating fashion (Table 1). THg concentrations in back feathers linearly increased with age,  
250 and did not differ between sexes (Table 1).

251 Our “animal models” revealed that individual repeatability was higher for back feather  
252 THg than blood THg concentrations (posterior mode  $R_{\text{feather Hg}} = 0.641$ , 95% CI [0.478, 0.722],  
253  $R_{\text{blood Hg}} = 0.191$ , 95% CI [0.102, 0.282], Table 1, Fig. 1). This difference in repeatability largely  
254 stemmed from differences in the magnitude of individual (permanent environment) effects:  
255 while individual effects accounted for 22% of the total phenotypic variance in back feather THg  
256 concentrations, they only did so for about 9% in blood THg concentrations (Table 1, Fig. 1).  
257 Additionally, in back feather samples, variation in individuals within years accounted for an  
258 additional 22% of the total variance (Table 1, Fig. 1).

259 In terms of additive genetic effects, our analysis demonstrated that there were heritable  
260 differences contributing to variation in mercury levels in both blood and back feathers (Table  
261 1, Fig. 1 and S1). When we standardized these additive genetic variances by the total phenotypic  
262 variance or mean, we found the heritability to be  $\sim 9\%$ , and the evolvability  $\sim 2\%$  for both traits.  
263 Finally, variation across years accounted for 12% and 40% of the total phenotypic variance of  
264 THg concentrations in back feathers and blood, respectively (Table 1, Fig. 1).

265 Finally, we applied a bivariate “animal model” to test for a correlation between THg  
266 concentrations in blood and back feathers, and to partition it into its underlying components.  
267 The results indicated that there was no significant correlation between both THg concentrations  
268 at the additive genetic (posterior mode  $r_{\text{genetic}} = -0.054$ , 95% CI [-0.455, 0.578]) or at the year  
269 level (posterior mode  $r_{\text{year}} = 0.109$ , 95% CI [-0.526, 0.709]) (Supplementary material, Table

270 S1). However, we may lack the statistical power to detect small correlations with high precision.  
271 At the individual (permanent environment) level, however, the correlation between the THg  
272 concentrations in blood and back feathers was significantly positive (posterior mode  $r_{individual} =$   
273 0.296, 95% CI [0.011, 0.533], Table S1, Figure 2).

274

## 275 **DISCUSSION**

276 In this study, we combined seven years of longitudinal data on THg concentrations measured  
277 in blood and back feathers of >600 common terns with information on the relatedness among  
278 these birds to explore the quantitative genetic architecture of these traits in this long-lived top-  
279 predator. We found that individual THg concentrations were repeatable, heritable and positively  
280 correlated, providing one of the first answers to the still largely unexplored questions about the  
281 adaptive potential of wild populations to global changes, such as increasing environmental  
282 pollution.

283 While the individual repeatability of back feather THg concentration was 64%, it was  
284 only 19% for blood. Interestingly, however, additive genetic variation was of a very similar  
285 magnitude in blood and back feathers, quantified both as the heritability and evolvability  
286 (approximately 9% and 2% for both traits, respectively). As such, the pronounced difference in  
287 repeatability between the tissues originates from the much higher among-individual (permanent  
288 environmental and among-individual within year) variance in THg concentration in back  
289 feathers compared to blood samples (permanent environmental/individual variance explained  
290 approximately 22% and 9% of total variance for blood and back feathers, respectively, Fig. 1).  
291 This makes sense, because blood THg concentrations during breeding should be strongly  
292 influenced by the contamination levels of the Banter See area, given that terns seem to forage  
293 within c. 20 km of the colony (Militão et al., 2023). Back feather THg concentrations on the  
294 other hand should be strongly influenced by the contamination levels of the vastly variable  
295 wintering areas of these same birds (Kürten et al., 2022). Indeed, these wintering areas were

296 recently found to be highly individually repeatable (98%; Kürten et al., 2022), as well as, using  
297 a subset from the feathers analysed here, to be subject to strongly different levels of mercury  
298 pollution (Bertram et al., 2022).

299 Individuals with higher THg concentrations in their blood exhibited higher  
300 concentrations in their back feathers at the phenotypic level. The not-different-from-zero  
301 correlation at the additive genetic level indicated that the observed link between blood and back  
302 feather THg concentrations was not driven by a shared genetic component, which could have  
303 risen due to pleiotropic effects of genes and/or linkage disequilibrium (Falconer and Mackay,  
304 1996). On the contrary, the positive correlation at the individual (permanent environment) level  
305 suggests that shared environmental factors are the main drivers of the observed correlation at  
306 the phenotypic level. One such shared environmental factor could be related to consistent (non-  
307 genetic) differences in foraging strategies among individuals in their breeding and wintering  
308 areas (Ceia and Ramos, 2015). Individuals proficient in hunting or occupying a higher trophic  
309 position in the breeding area (i.e., capable of preying on larger fish, which might be more  
310 nutritious but also have accumulated higher mercury levels) might employ similar foraging  
311 strategies in the wintering area. While this is a highly plausible explanation, further research  
312 should help to elucidate the nature of the observed correlation in mercury prevalence between  
313 tissues. For instance, a comprehensive study of stable isotopes could help to determine the level  
314 of variation in diet composition among individuals, and across breeding and wintering areas.

315 Although our study provides solid evidence for the repeatability, heritability,  
316 evolvability and a correlation structure in THg concentrations measured in two different tissues,  
317 we cannot at present provide a compelling explanation as to what “trait” we have quantified.  
318 For instance, THg concentrations might be the product of variation in behavioural traits linked  
319 to susceptibility (e.g., uptake differences due to foraging strategies or areas; Renedo et al., 2018;  
320 Dodino et al., 2022) and/or physiological traits (e.g., additional storage (Eagles-Smith et al.,  
321 2009; Robinson et al., 2011) or excretion mechanisms besides feathers (Lewis and Furness,

322 1993; Ackerman et al., 2016)). With respect to the latter, preliminary results from a limited  
323 dataset of mercury concentrations measured using faecal samples (n=6) suggests that faecal  
324 excretion may not be a major contributor to mercury detoxification (Table S2). This is  
325 consistent with findings from a study on little penguins (*Eudyptula minor*, Finger et al., 2017),  
326 but overall evidence seems to be mixed (Lewis and Furness, 1991), emphasizing the need for  
327 further research on the topic. For females, mercury excretion through eggs could be an  
328 additional source of variation among and within individuals during the breeding season  
329 (Ackerman et al., 2016), something that calls for further investigation to obtain a better  
330 understanding of the biological meaning of our metric of mercury contamination, for example  
331 by repeatedly sampling eggs of individual females across years to assess the repeatability of  
332 mercury excretion via egg laying. Assessing variation in mercury deposition in the liver,  
333 however, would require sacrificing birds to obtain samples, thereby precluding repeated  
334 sampling, and ultimately preventing the assessment of variation among and within individuals.  
335 Finally, it is important to highlight that our study focused on the quantitative genetics of  
336 mercury levels using samples from back feathers, and that our conclusions might not be  
337 generalizable to other types of feathers, such as primary or tail feathers, the collection of which  
338 we deemed too invasive. Further research, perhaps using carcasses, should assess correlations  
339 among mercury concentrations among feather types within individuals.

340 Numerous previous studies have shown detrimental effects of mercury on avian  
341 reproduction via direct embryo toxicity (Heinz and Hoffmann, 2003; Herring et al., 2010), as  
342 well as impairments of development (Amélineau et al., 2019) or survival of chicks (Goutte et  
343 al., 2014; Whitney and Cristol, 2017), highlighting its ecological significance. However, to our  
344 knowledge, no study to date has been able to disentangle mercury contamination resulting from  
345 environmental factors from that resulting from genetically fixed differences in susceptibility to  
346 mercury contamination in wild birds. In this study, we investigated the heritability and  
347 evolvability of mercury susceptibility, providing pioneering evidence about its evolutionary

348 significance in a natural population. If mercury sensitivity is underpinned by a genetic  
349 component and linked to fitness, it should be able to evolve in response to selection, leading to  
350 adaptive potential of populations in response to global changes, such as increasing  
351 environmental contamination.

352

### 353 **ETHICS**

354 This work was carried out under the license of the city of Wilhelmshaven as well as animal  
355 experimentation licenses granted by the Lower Saxony State Office for Consumer Protection  
356 and Food Safety, Germany.

357

### 358 **DATA ACCESSIBILITY**

359 Data will be archived in the Dryad Digital Repository upon acceptance of the manuscript.

360

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525 **TABLES**

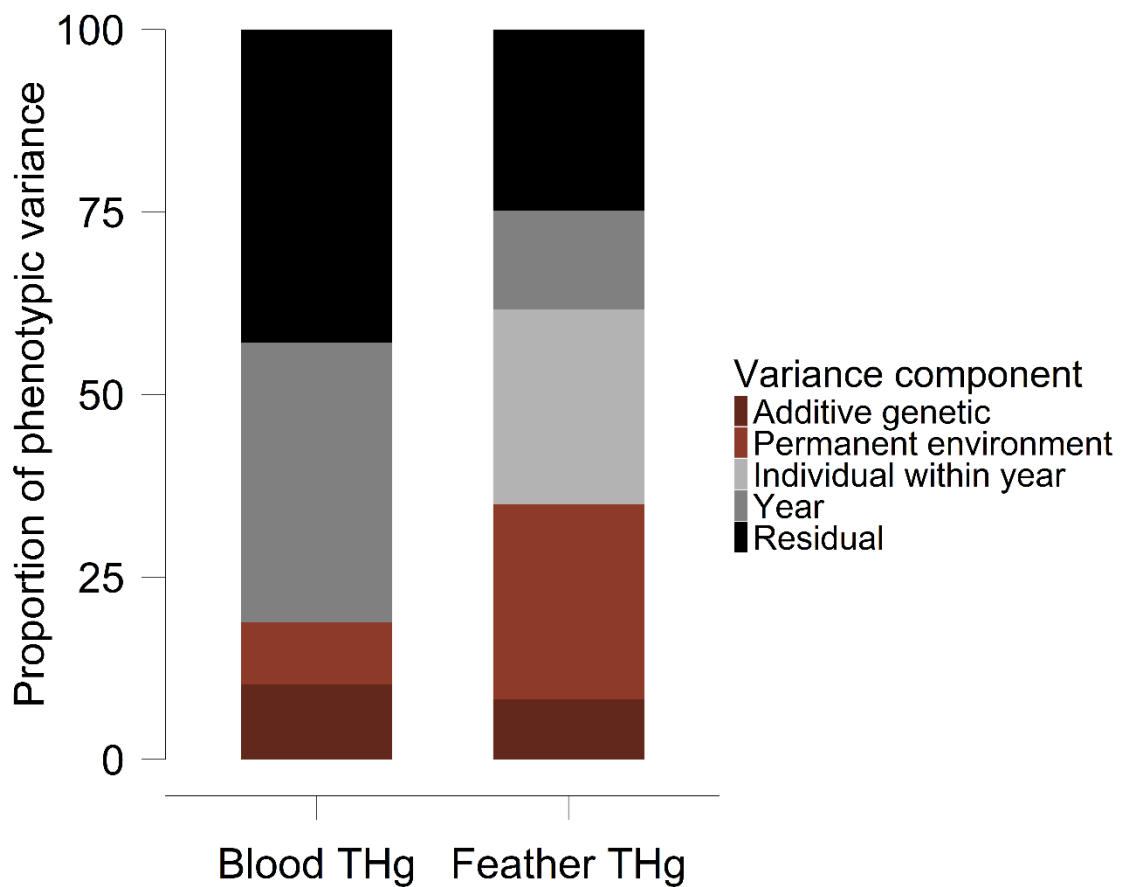
526 **TABLE 1.** Estimates from two univariate mixed-effects “animal models” applied to investigate  
 527 sources of phenotypic variation in total mercury (THg) concentrations measured in blood and  
 528 back feathers of >600 common terns from a natural population. Point estimates of fixed and  
 529 random effects are shown as posterior modes, (posterior medians) and [95% credible intervals].

	<b>(log) Blood THg</b>		<b>(log) Back feather THg</b>	
	<b>Estimate</b>	<b>95% CI</b>	<b>Estimate</b>	<b>95% CI</b>
<b>Fixed effects</b>				
Intercept	6.633 (6.628)	[6.441, 6.818]	7.553 (7.534)	[7.27, 7.798]
Age [linear]	0.047 (0.046)	[0.034, 0.060]	0.068 (0.067)	[0.038, 0.093]
Age [quadratic]	-0.001 (-0.001)	[-0.002, -0.001]	-0.002 (-0.001)	[-0.003, 0.000]
Sex [female]	-0.267 (-0.267)	[-0.299, -0.232]	-0.045 (-0.029)	[-0.12, 0.063]
<b>Random effects</b>				
Additive genetic	0.011 (0.012)	[0.004, 0.019]	0.024 (0.027)	[0.01, 0.049]
Individual	0.009 (0.010)	[0.004, 0.018]	0.065 (0.062)	[0.03, 0.090]
Individual within year	-	-	0.089 (0.090)	[0.069, 0.111]
Year	0.038 (0.048)	[0.014, 0.134]	0.033 (0.041)	[0.009, 0.130]
Residual	0.047 (0.047)	[0.042, 0.051]	0.067 (0.066)	[0.061, 0.072]
<b>Standardized variance metrics</b>				
Repeatability	0.191 (0.191)	[0.102, 0.282]	0.641 (0.624)	[0.478, 0.722]
Heritability	0.097 (0.096)	[0.025, 0.178]	0.073 (0.089)	[0.037, 0.172]
Evolvability	1.512 (1.580)	[1.005, 2.077]	1.932 (2.032)	[1.374, 2.860]



531 **FIGURES**

532 **FIGURE 1.** Bar plot showing the proportion of total phenotypic variance explained by the  
533 different variance components of total mercury (THg) concentrations measured in blood and  
534 back feathers of >600 common terns from a natural population. Additive genetic effects are  
535 shown in dark red, permanent environmental effects in red, individual within year effects in  
536 light grey, year effects in dark grey, and residual variance components in black. Given that  
537 variance components are standardised by the total phenotypic variance, the additive genetic  
538 effect represented in the figure equals to the heritability, while the sum of the additive genetic  
539 and permanent environmental effects for blood THg concentrations, and that of the additive  
540 genetic, permanent environmental and individual within year effects for back feather THg  
541 concentrations equals to the repeatability.



543 **FIGURE 2.** Best linear unbiased predictors (BLUPs) of individual values for blood and back  
544 feather total mercury (THg) concentrations, as extracted from the bivariate mixed-effects  
545 “animal model” presented in Table S1. The solid green line represents the individual  
546 (permanent environment) correlation, the shaded area the 95% confidence interval and the  
547 dashed line the  $x=y$  line. Note that this figure is drawn for illustrative purposes only,  
548 conclusions were drawn directly from the model estimates (Table S1).

