

Quantitative meta-analysis reveals no association between mercury contamination and body condition in birds

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14 Quantitative meta-analysis reveals no association between

15 mercury contamination and body condition in birds

16

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- 56
- 57 ABSTRACT

58 Mercury contamination is a major threat to the global environment, and is still increasing in

- 59 some regions despite international regulations. The methylated form of mercury is hazardous
- 60 to biota, yet its sublethal effects are difficult to detect in wildlife. Body condition can vary in
- 61 response to stressors, but previous studies have shown mixed effects of mercury on body

62 condition in wildlife. Using birds as study organisms, we provide the first quantitative 63 synthesis of the effect of mercury on body condition in animals. In addition, we explored the influence of intrinsic, extrinsic and methodological factors potentially explaining cross-study 64 65 heterogeneity in results. We considered experimental and correlative studies carried out in adult birds and chicks, and mercury exposure inferred from blood and feathers. Most 66 67 experimental investigations (90%) showed a significant relationship between mercury 68 concentrations and body condition. Experimental exposure to mercury disrupted nutrient (fat) 69 metabolism, metabolic rates, and food intake, resulting in either positive or negative 70 associations with body condition. Correlative studies also showed either positive or negative 71 associations, of which only 14% were statistically significant. Therefore, the overall effect of 72 mercury concentrations on body condition was null in both experimental (estimate \pm SE = 73 0.262 ± 0.309 , 20 effect sizes, five species) and correlative studies (-0.011 ± 0.020 , 315 effect 74 sizes, 145 species). The single and interactive effects of age class and tissue type were 75 accounted for in meta-analytic models of the correlative data set, since chicks and adults, as 76 well as blood and feathers, are known to behave differently in terms of mercury accumulation 77 and health effects. Of the 15 moderators tested, only wintering status explained cross-study 78 heterogeneity in the correlative data set: free-ranging wintering birds were more likely to 79 show a negative association between mercury and body condition. However, wintering effect 80 sizes were limited to passerines, further studies should thus confirm this trend in other taxa. 81 Collectively, our results suggest that (1) effects of mercury on body condition are weak and 82 mostly detectable under controlled conditions, and (2) body condition indices are unreliable 83 indicators of mercury sublethal effects in the wild. Food availability, feeding rates and other 84 sources of variation that are challenging to quantify likely confound the association between 85 mercury and body condition in natura. Future studies could explore the metabolic effects of mercury further using designs that allow for the estimation and/or manipulation of food intake 86

| 87 | in both wild and captive birds, especially in under-represented life-history stages such as |
|-----|---|
| 88 | migration and overwintering. |
| 89 | |
| 90 | Key words: blood, body mass, fat, feather, feeding, energetics, habitat, metabolism, species. |
| 91 | |
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117

118 I. INTRODUCTION

119 Chemical pollution is a major anthropogenic modification of the global environment, 120 and a fundamental characteristic of the Anthropocene (Lewis & Maslin, 2015). Humans are 121 responsible for the synthesis and release of a plethora of chemical contaminants for 122 agricultural uses [e.g. organochlorine and organophosphate pesticides (Jones & De Voogt, 123 1999; Sánchez-Santed, Colomina & Herrero Hernández, 2016)], and industrial or every-day 124 life applications [e.g. metallic trace elements, perfluoroalkyl substances, chlorinated paraffins 125 (Walker et al., 2012; Vorkamp et al., 2019; Sunderland et al., 2019)]. Among these 126 contaminants, and despite being a natural element, mercury (Hg) is particularly hazardous to 127 humans and wildlife because it has no biological function and is highly toxic even at low concentrations (Walker et al., 2012; UN Environment, 2019). In its inorganic form, Hg has an 128 129 atmospheric lifetime of 0.5-1 year and can be transported over vast spatial scales (Obrist *et* 130 al., 2018; UN Environment, 2019). Once deposited on the Earth's surface, Hg can undergo 131 complex, microbially mediated processes and be converted into methylmercury (MeHg), 132 which is assimilated and accumulated by living organisms, and biomagnifies in food webs 133 (Atwell, Hobson & Welch, 1998; Evers et al., 2016; Eagles-Smith et al., 2018). 134 Anthropogenic Hg emissions have declined in North America and Europe over the 135 past two decades (UN Environment, 2019), but are still increasing in East Asia and in the 136 Southern Hemisphere (Obrist et al., 2018). In addition, concentrations measured in wildlife

137 are still increasing in several regions of the Northern (Braune et al., 2014; Wang et al., 2019) 138 and Southern Hemispheres (Seco et al., 2020; Mills et al., 2020). The Minamata Convention, 139 an international treaty that came into force in 2017 (http://www.mercuryconvention.org), 140 adopted a global strategy to reduce Hg emissions and protect human and environmental 141 health. While these global restrictions may limit increases in future Hg emissions linked to 142 economic growth, legacy Hg emissions will continue to affect the Hg cycle for decades to 143 centuries (Eagles-Smith et al., 2018). Monitoring Hg concentrations and effects in biota and 144 the environment is thus a priority to oversee the effectiveness of the Minamata Convention 145 (Evers et al., 2016).

146 Adverse effects of Hg in humans and wildlife include neurological, endocrine, and immune disruption with consequences on development, neurocognitive function, and 147 reproduction (Tchounwou et al., 2003; Heinz et al., 2009; Tan, Meiller & Mahaffey, 2009; 148 149 Tartu et al., 2013; Goutte et al., 2014; Evers, 2018; Eagles-Smith et al., 2018). Several 150 intrinsic and extrinsic factors drive variation in Hg contamination and kinetics in wild 151 organisms. Feeding ecology is a key explanatory factor of among- and within-species 152 variation in tissue Hg concentrations (Anderson et al., 2009; Carravieri et al., 2014b, 2021; Polito et al., 2016; Ma et al., 2021) but other traits such as sex and age can also modulate this 153 154 variation (Eagles-Smith et al., 2009; Robinson, Lajeunesse & Forbes, 2012; Jackson et al., 155 2015; Chételat et al., 2020). In addition, life-history traits such as breeding or migration 156 strategies can influence diet, feeding rate, energy storage and expenditure, thus driving variation in Hg burdens (Seewagen, Cristol & Gerson, 2016; Ackerman, Hartman & Herzog, 157 158 2019; Adams et al., 2020a). All these intrinsic and extrinsic factors thus have the potential to 159 modulate Hg toxicity. However, identifying sublethal effects of Hg in the field can be 160 challenging, due to the potentially confounding influence of concurring environmental 161 stressors (Marcogliese & Pietrock, 2011; Marteinson, Marcogliese & Verreault, 2017;

Bårdsen, Hanssen & Bustnes, 2018). Studies have shown species-specific sensitivity to Hg
toxicity [e.g. embryotoxicity in birds (Heinz *et al.*, 2009); neuroreceptor inhibition in
mammals (Basu *et al.*, 2005)], but the key phylogenetic and life-history traits or
environmental factors that could explain these differences have yet to be identified clearly.
Meta-analytical approaches quantifying the link between Hg and health endpoints in a large
number of taxa could be effective in identifying the interactive factors that limit our capacity
to detect significant effects of Hg on wildlife health.

169 Here, we performed a meta-analysis investigating the effect of Hg contamination on body condition using information extracted from 47 studies on 147 species of birds. Body 170 171 condition indices are available in a large number of studies and species, and they can be 172 calculated from morphometric measures that are used routinely in avian investigations. Albeit 173 widely used, body condition indices may not be reliable indicators of health status (Fischer, 174 Taborsky & Dieckmann, 2009; Schultner et al., 2013). Here, we consider body condition as 175 an integrative measure of fat and lean mass (Peig & Green, 2009; Labocha & Hayes, 2012) 176 that can be affected linearly or non-linearly by stressors (Pravosudov & Grubb, 1997; 177 Schultner et al., 2013), for example via changes in behaviour (e.g. feeding performance) and/or physiology (e.g. disruption of nutrient metabolism and energy use). We chose birds as 178 179 the study taxon because they have served widely as early sentinels of negative effects of Hg 180 on wildlife and ecosystem health (Wolfe, Schwarzbach & Sulaiman, 1998; Whitney & 181 Cristol, 2018). Birds are ubiquitous, being found in a large variety of terrestrial, freshwater 182 and marine habitats from polar regions to the tropics. In addition, they belong to different 183 dietary guilds, from herbivores to omnivores, are relatively accessible compared to other 184 groups of vertebrates, and are thus extensively studied (Konishi et al., 1989). Our aim was 185 twofold: (1) to test for a systematic trend in the effect of Hg on body condition in birds; and 186 (2) to identify moderators of this relationship among intrinsic (e.g. species, age class, sex) and 187 extrinsic factors (habitat type, dietary guild), as well as methodological aspects (tissue used to 188 measure Hg concentrations, correlative or experimental approach). As Hg can affect bird 189 behaviour [e.g. reduced ability to forage and/or compete for food (e.g. Evers et al., 2008)], 190 metabolic rates (Gerson, Cristol & Seewagen, 2019), and physiological pathways involved in 191 the stress response (Wada et al., 2009; Franceschini et al., 2017), which can have a range of 192 contrasting consequences for physical condition, we expected either a positive or negative 193 relationship between Hg concentrations and body condition. Given Hg biomagnification and 194 naturally high bioavailability in aquatic environments (Atwell et al., 1998; Fitzgerald, 195 Lamborg & Hammerschmidt, 2007), piscivorous species can be at greater risk of Hg exposure 196 (Scheuhammer *et al.*, 2007), and are thought to have developed a better tolerance to toxicity 197 over evolutionary timescales [e.g. through more efficient detoxification mechanisms (Robinson et al., 2011; Manceau et al., 2021)]. Piscivorous species might therefore show a 198 199 smaller effect size of the Hg-body condition association.

200

201 II. MATERIALS AND METHODS

202 (1) Search and inclusion criteria

203 Our literature search was conducted in ISI Web of Science (latest search 22/01/2021) across all years, using the search terms "mercury", "bird" and "body condition". Since body 204 205 condition is often calculated in studies of the effect of Hg on physiological and fitness 206 endpoints without being the primary objective, we also searched the literature using the terms "mercury", "bird" and one of the following key words: "effect", "health", "telomere", 207 208 "oxidative stress", "hormone", "corticosterone", "testosterone", "thyroid", "immunity", "parasite", "DNA damage", "energy", "hatching/fledging/breeding success", "hatch date", 209 "clutch size", "foraging behaviour", "survival", "growth" and "body mass". The reference 210 211 lists of literature reviews found in this way were also checked to expand the database (Fig. 1). 212 We contacted the authors of studies to obtain further details when (i) statistical information 213 was missing, and/or (ii) the effect size was calculated across several species. Incomplete 214 statistical information and a lack of a response by contacted authors meant that some relevant 215 studies had to be discarded (see online Supporting Information, Table S1). The literature 216 search resulted in the selection of 47 studies spanning publication years 2000 to 2020 (Table 217 1). These covered data mainly on passerines and seabirds with a few waders and raptors 218 (Table 1). In addition, we included nine studies from the authors' unpublished work in order 219 to reduce the bias towards passerine birds. Overall, our meta-analysis included 147 species of 220 birds, which were mainly passerines and seabirds. Inclusion criteria are detailed below.

221

222 (a) Body condition indices

223 Previous studies attempting to determine which body condition index better represents 224 fat and/or lean mass have produced mixed results in both mammals and birds (e.g. Labocha, 225 Schutz & Hayes, 2014; Kraft et al., 2019). Here, variables initially retained as pertinent 226 indices of body condition were: size-corrected body mass (e.g. scaled mass index (SMI), 227 structural size to body mass ratio, residuals of an ordinary least-squares regression of body 228 mass against a linear morphometric measure of size), body mass, organ-to-body ratio, fat 229 scores, pectoral muscle thickness, and organ masses. However, only eight effect sizes from 230 four studies were estimated from indices other than size-corrected body mass or body mass 231 (Table S1), preventing an accurate estimation of their potential influence on the Hg–body 232 condition relationship. Therefore, these effect sizes were not included in meta-analytic 233 models. The majority of published articles from which effect sizes were extracted used SMI 234 (Peig & Green, 2009) as body condition index (see Table S2 for the frequency of all condition 235 indices). Therefore, to minimise data heterogeneity, we also calculated SMI as the body 236 condition index when we had access to raw data. The SMI has several advantages over other

indices because it is not size dependent and can be used readily to compare across populations
(Labocha *et al.*, 2014). The SMI adjusts the mass of the individuals to the mass they would
have if all individuals had the same body size, using the following equation:

$$\dot{M}_i = M_i \, L_0^{b \text{SMA}} / L_i$$

241 where M_i and L_i are the body mass and the body length measure of individual *i*, respectively; 242 the exponent b_{SMA} is estimated by the standardised major axis (SMA) regression of log body 243 mass on log body length; L_0 is an arbitrary value of body length, and \dot{M}_i is the predicted body 244 mass for individual i when the body length is standardised to L_0 . We calculated L_0 as the 245 arithmetic mean of the body length variable chosen for each study. As different measures of 246 body length (e.g. tarsus, bill, and wing length) can scale differently with body mass depending 247 on species, we used the body size measure selected by the authors to calculate L_0 and thus 248 SMI. When no preference was communicated, and several body length measures were 249 available, we used tarsus or bill length rather than wing length, which is difficult to measure 250 reproducibly and can be a poor indicator of structural body size (Jenni & Winkler, 1989). The 251 choice between tarsus or bill length was made by taking the measure that correlated better 252 with body mass on a log basis, as this is likely to be the best one explaining the fraction of 253 mass associated with structural size (Peig & Green, 2009).

254

255 (b) Hg chemical form

The form of Hg in avian diets may vary depending on prey types. High-trophic-level
prey, such as fish and squid, mainly contain Hg as MeHg, whereas invertebrates may have
higher proportions of inorganic Hg (Bloom, 1992; Mason, Laporte & Andres, 2000;
Bustamante *et al.*, 2006; Seco *et al.*, 2020). All included studies measured total Hg, which is
an accurate proxy of MeHg in tissues such as blood and feathers (e.g. Bond & Diamond,
2009; Renedo *et al.*, 2021).

262

263 (c) Exposure pathway and measure

We included experimental studies where adults and chicks were exposed to Hg via 264 dietary exposure as MeHg, as well as MeHg egg injections. We considered studies where Hg 265 266 contamination was inferred from concentrations [in parts per million (ppm) or µg per unit wet 267 or dry mass) measured in whole blood, red blood cells, and feathers, in adult birds and chicks. 268 We excluded effect sizes obtained from other tissues given their heterogeneity and small 269 number (Table S1). In experimental studies all Hg concentrations were reported on a wet 270 mass basis. By contrast, the majority of correlative studies reported Hg concentrations on a 271 dry mass basis. In order to provide homogenous Hg concentration estimates, correlative 272 studies presenting results on a wet mass basis were converted to dry mass. The latter 273 calculation was based on a moisture content of 65% in red blood cells (P. Bustamante, O. 274 Chastel unpublished data), and 77% in whole blood [mean of moisture values measured in 275 Eagles-Smith et al. (2008), Ackerman, Hartman & Herzog (2017) and Ackerman et al. 276 (2019). Blood is a better representative of Hg body burden than are feathers in birds, and 277 should be preferred in toxicity risk estimations (Fuchsman et al., 2017; Chételat et al., 2020). 278 In addition, Hg temporal integration into feathers can be highly variable depending on 279 species, feather type, moult strategy and moult stage at sampling (Carravieri et al., 2014a; 280 Peterson et al., 2019; Albert et al., 2019). However, in some species, feather Hg 281 concentrations correlate well with concentrations in internal tissues, including blood, and can 282 thus also be useful representatives of Hg body burdens (Ackerman et al., 2012, 2019; Fort et 283 al., 2014). Therefore, we decided to include studies reporting associations between feather Hg 284 concentrations and body condition in our meta-analysis, and test tissue type (blood or feather) 285 as a moderator. Body feathers are preferentially sampled for ethical and practical reasons,

and, to avoid further heterogeneity in the data set, we excluded the few effect sizes obtainedfrom other feather types (Table S1).

288

289 (d) Other criteria

Studies comparing body condition indices between populations at polluted sites where pollution was not clearly Hg-related were also excluded, as well as studies on dead, emaciated individuals (Table S1), where body condition could be biased. Effect sizes obtained from less than four individual birds were discarded.

294

295 (2) Moderators included and categorisation

296 Our meta-analysis included a maximum of 15 moderators: (1) bird type (passerine, raptor, seabird, wader); (2) age class (chick, adult); (3) whether the effect size had been 297 298 corrected for sex; (4) whether the effect size had been corrected for other factors that were 299 specific to the study (e.g. individual random factor, sampling date, season); (5) dietary guild 300 (carnivore, herbivore, invertivore, omnivore); (6) habitat type (freshwater, marine, terrestrial); 301 (7) geographical zone (polar/subpolar, temperate, tropical/subtropical); whether the sampled 302 population was (8) wintering (yes/no), (9) migrating (yes/no) or (10) breeding (yes/no); (11) 303 tissue type used for Hg quantification (blood, feather); (12) body condition index (body mass, 304 size-corrected body mass); (13) species-specific basal metabolic rate (BMR); (14) Hg 305 concentration; (15) ratio of species-specific maximum body mass to average body mass 306 (hereafter BM ratio, which reflects the maximum body condition of the species; Vincze et al., 307 2019). All moderators, their modalities, the number of effect sizes, and the justification for 308 including them to study the link between Hg concentration and body condition are reported in 309 Table 2. Dietary guild was assigned based on results in the sampled population of each study 310 when available, or from the Wilman et al. (2014) database. Species-specific BMR values

| 311 | were extracted from Ellis & Gabrielsen (2001), Møller (2009), Londoño et al. (2015) and |
|-----|--|
| 312 | McKechnie, Noakes & Smit (2015), but were not available for all species. Body mass |
| 313 | information to calculate the BM ratio was extracted from the Dunning (2007) database, or |
| 314 | from additional references (Glahn & McCoy, 1995; Shirihai et al., 2002; Kooyman et al., |
| 315 | 2004; Helseth, Stervander & Waldenström, 2005; Tobón & Osorno, 2006; Kojadinovic et al., |
| 316 | 2007a; Overton et al., 2009; Rising, 2010; Hancock, Kushlan & Kahl, 2010; García, Moreno- |
| 317 | Opo & Tintó, 2013; Maccarone & Brzorad, 2016; studies included in the meta-analysis). For |
| 318 | each study, we extracted the moderators, as well as sample and effect sizes as detailed below. |
| 319 | |
| 320 | (3) Effect size extraction or calculation |
| 321 | Given that most studies were correlative, we chose Pearson's r as the effect size. |
| 322 | Based on the information given in correlative studies, we calculated effect sizes using <i>t</i> - |
| 323 | values, F-values, P-values, means and standard deviations, or correlation coefficients, |
| 324 | following formulae given in Koricheva, Gurevitch & Mengersen (2013). For studies reporting |
| 325 | the comparison of experimental groups, we calculated standardised mean differences |
| 326 | (Cohen's d), which were then transformed to Pearson's r , following Koricheva <i>et al.</i> (2013). |
| 327 | To adhere to normality assumptions, Pearson's r were then converted to Fisher's Zr following |
| 328 | the equation in Lipsey & Wilson (2001). Sampling variances associated Z-scores were |
| 329 | calculated as $(n-3)^{-1}$ following Koricheva <i>et al.</i> (2013). Positive effect sizes indicate a |
| 330 | positive effect of Hg on body condition, while negative effect sizes denote a decrease in body |
| 331 | condition with increasing Hg concentrations. |
| 332 | |
| 333 | (4) Meta-analytic technique |
| | |

In a preliminary step, we conducted a meta-analysis on the full data set including 335
effect sizes and a study type moderator (correlative or experimental) (results not shown).

336 However, experimental studies appeared to be highly influential in the effect estimates,

337 because of extreme values and high leverage. Therefore, we carried out separate meta-

analyses for correlative and experimental data sets.

339

340 (a) Potential bias in effect size reporting

341 To test for the presence of potential bias in the results of our meta-analysis, we first 342 explored funnel plots produced between effect sizes and their corresponding measure of 343 precision (here standard error, SE) for signs of asymmetry. Second, we performed Egger's regression tests (Egger et al., 1997) using overall intercept-only models with the regtest 344 345 function (metafor package, v. 2.4-0; Viechtbauer, 2010). Egger's test evaluates the 346 relationship between effect sizes and measurements of study precision (Egger et al., 1997), 347 and can reveal different types of bias, such as reporting bias or poor methodological quality 348 (Sterne et al., 2011). For instance, studies reporting a significant effect may be more likely to 349 be published than studies reporting no effect (Koricheva et al., 2013; but see Koricheva, 350 2003). Here, most effect sizes for correlative studies, and all effect sizes for experimental 351 studies, were extracted from published resources (Fig. 1). Our meta-analysis also included 352 unpublished resources for the correlative data set. We thus tested (1) potential bias in 353 published and unpublished studies separately, as well as combined; (2) whether the 354 publication status (used as a moderator) of the effect size had an effect on the meta-analytical 355 results.

356

357 (b) Random structure and overall effect of Hg on body condition

All meta-analytic models were performed using the *rma.mv* function in the *metafor* package (v. 2.4-0; Viechtbauer, 2010) in R (v. 4.0.5; R Core Team, 2021). We constructed multilevel meta-analytic linear mixed effect models, which facilitates the control of multiple 361 sources of non-independence. Our data were affected by multiple types of non-independence 362 (Noble et al., 2017), including non-independence of effect sizes, multiple effect sizes originating from the same studies, non-independence of observations of the same species, as 363 364 well as non-independence of species (shared ancestry). We aimed to control for these 365 dependencies by testing the effect of three random variables: individual effect size identity 366 (individual effect size ID, unique per data row, necessary to estimate residual heterogeneity; 367 Noble et al., 2017), study identity (study ID), and species identity (species ID). In the 368 correlative data set, we also tested the influence of the phylogenetic variance-covariance matrix representing the phylogenetic history of the species. For the latter, we used a rooted 369 370 ultrametric consensus tree that was inferred from the SumTrees Python library (Sukumaran & 371 Holder, 2010), based on 1,000 random trees obtained from birdtree.org (Jetz et al., 2012), 372 using the Hackett backbone tree (Hackett et al., 2008). Phylogeny was not accounted for in 373 the experimental data set, as including phylogenetic random effects with less than 15 species 374 can lead to unreliable estimates (Bolker et al., 2009). To select the appropriate random 375 structure, we constructed intercept-only meta-regression with all combinations of the three 376 random variables, as well as the phylogenetic signal for correlative studies, using the 377 maximum-likelihood (ML) method. We then compared the models using the Akaike 378 Information Criterion (AIC) and chose the random structure of the model with the lowest AIC 379 value, and lowest number of variables when AIC values were similar between models 380 (parsimony criteria) (Table S3). Using the random structure of the best selected model, we 381 tested the overall effect size of Hg contamination on body condition using restricted 382 maximum likelihood approximation (REML). We also calculated the heterogeneity statistic (I^{2}_{total}) based on an intercept-only meta-analytic model (built using the rma function in 383 *metafor*), without any random effects. I^2 represents the percentage heterogeneity in the effect 384 sizes (0–100%) due to true heterogeneity rather than random sampling variance (Higgins & 385

Thompson, 2002; Higgins *et al.*, 2003). I^2 was moderate to high (defined as $I^2 > 50\%$; Higgins *et al.*, 2003, see Section III), therefore we ran moderator analyses to explore which lifehistory, ecological or physiological parameters could explain the high heterogeneity observed in the effect of Hg contamination on body condition in birds.

390

391 (c) Moderator analysis

392 In order to study the influence of different moderators on the association between Hg 393 contamination and body condition, we constructed multifactorial meta-analytic models using 394 the MuMIn package (Bartón, 2020). Chicks and adults, as well as blood and feathers, are 395 known to behave differently in terms of Hg accumulation and health effects (e.g. Whitney & 396 Cristol, 2018), and could show different associations between Hg and body condition. 397 Therefore, their single and interactive effects were always accounted for in models of the 398 correlative data set, as follows: Z score \sim age class + tissue type + age class * tissue type + 399 Moderator (Table S4). Models were constructed with the selected random structure (see 400 Sections II.4b and III), fitted using ML, and compared to the base model: Z score ~ age class 401 + tissue type + age class*tissue type. In preliminary steps the age class 'juveniles' was considered, but data were too scarce to enable inclusion in the final meta-analysis. The 402 403 available data on body condition and Hg concentrations in blood or feathers of juveniles were 404 pooled with those of adults. We considered that a moderator had a significant effect on the 405 association between Hg and body condition when its addition to the base model decreased the 406 AIC corrected for small sample size (AICc) by at least 2. Data on BMR were available only 407 for a subset of observations. To test the effect of BMR on the association between Hg and 408 body condition we thus constructed a separate set of models (Table S4). Using these models, 409 we obtained parameter estimates for each predictor after refitting models with REML.

The experimental data set was too small for multifactorial statistical analysis (*N* = 20
effect sizes). Therefore, each moderator was entered as a single predictor to an intercept-only
multilevel meta-analytic model (fitted by REML) with the selected random structure (Table
S5). Using these models, we obtained parameter estimates for each predictor and factor level.
The overall significance of each predictor was assessed using an omnibus test (Viechtbauer,
2010).

416

417 III. RESULTS

418 (1) Bias in effect size reporting

419 For the correlative data set, Egger's tests indicated a tendency for biased reporting

420 towards negative effect sizes among published studies (Egger's test: N = 224, z = -1.932, P =

421 0.053), and a significant bias towards positive effect sizes among unpublished studies

422 (Egger's test N = 91, z = 2.148, P = 0.032; see Table S6 for funnel plots). By contrast, we

423 found no statistical evidence of bias in the correlative database combining published and

424 unpublished effect sizes (Egger's test: N = 315, z = -0.707, P = 0.480). In addition,

425 publication status had no effect on the Hg–body condition association (Table S6). Therefore,

426 all further meta-analytic models were only run on the full correlative data set combining

427 published and unpublished effect sizes.

428 We detected a tendency for biased reporting towards negative effect sizes in 429 experimental studies (Fig. 2; Egger's test: N = 20, z = -1.894, P = 0.058), but this bias was

430 non-significant.

431

432 (2) Correlative studies

We used 315 population-specific effect sizes from 145 species to test the relationship
between Hg concentration and body condition in correlative studies. These were carried out in

435 wild populations, including mainly adult passerines and seabirds, from terrestrial and marine 436 environments, in temperate and polar/subpolar regions (Table 2). The median number of individuals inspected per effect size was 16 (range: 4-1051). Comparison of intercept-only 437 438 multilevel meta-analytic models indicated a significant increase in fit with the inclusion of 439 individual effect size ID and species ID (Table S3), which were retained in the random 440 structure of all subsequent models. Phylogenetic signal appeared to have little influence on 441 the overall effect size and did not affect model fit. The overall effect of Hg contamination on 442 body condition was non-significant (estimate \pm SE = -0.011 ± 0.020 , confidence interval, CI [-0.049; 0.027], while accounting for individual effect size ID and species ID). Effect size 443 heterogeneity was moderate ($I^2 = 55\%$; Cochran's Q test = 668, df = 314, P < 0.0001), 444 445 indicating suitability for moderator analyses. Multifactorial moderator analyses revealed that 446 wintering status had an influence on effect size estimates (AICc 2.6 points lower than the base 447 model, Table S4): wintering birds were more likely to show a negative effect of Hg on body 448 condition (Fig. 3). Other moderators had no clear effects on the Hg-body condition 449 association (Table S4).

450

451 (3) Experimental studies

Experimental studies encompassed 20 effect sizes from five species (*Ardea alba*, *Falco sparverius*, *Gavia immer*, *Setophaga coronata*, *Taeniopygia guttata*). The median number of individuals inspected per effect size was 24 (range: 5–49). Only individual effect size ID was retained in the random structure of intercept-only multilevel meta-analytic models (Table S3). Hg contamination was not related to body condition (0.262 ± 0.309 , [–0.344; 0.867], while accounting for individual effect size ID), and effect size heterogeneity was very high ($I^2 = 99\%$; Cochran's Q test = 887, df = 19, P < 0.0001). In the experimental data set, no 459 moderator predicted the Hg–body condition relationship (Table S5, Fig. 4, P > 0.100 in all 460 Omnibus tests).

461

462 IV. DISCUSSION

463 Our extensive meta-analysis showed no overall effect of Hg contamination on body 464 condition across 147 free-living or captive bird species. However, free-ranging wintering 465 passerines were more likely to present a negative association between Hg concentration and 466 body condition, but further studies are necessary to confirm this trend in other taxa. We found that waders and raptors, birds in freshwater habitats and tropical/subtropical regions, and 467 468 especially migrating and overwintering birds, are under-represented in the literature on Hg 469 contamination and body condition. Experimental studies were more likely to detect a 470 significant effect of Hg concentrations on body condition, with 90% of estimated effect sizes 471 being significantly positive or negative. Conversely, only 14% of correlative effect sizes for 472 the effect of Hg contamination on body condition were significantly positive or negative. 473 Although recent experimental studies exposed birds to environmentally realistic Hg doses, 474 these were often in the upper range of levels encountered in the wild (Kobiela, Cristol & Swaddle, 2015; Yu et al., 2016; Ma et al., 2018). Therefore, the difference in sensitivity to 475 476 effects between correlative and experimental studies could stem from a threshold dose that 477 can be reached under controlled conditions, but is unlikely in the wild.

478

479 (1) Overview of experimental and correlative studies

Accumulation of energy stores can be part of the response to stressors, whereby
perceived risk or unpredictable access to food can cause birds to store energy as a buffer
against unpredictable environmental changes [Schultner *et al.* (2013) and references therein].
Experimental exposure to environmentally realistic Hg levels caused an increase in energy

484 (fat) stores and body mass in zebra finch *Taeniopygia guttata* (Gerson *et al.*, 2019). Feeding 485 rate or ingested food were not quantified, but birds were offered food ad libitum. Hence, their increase in energy stores was likely linked to an increase in food intake, as shown in mallard 486 487 ducks Anas platyrhynchos exposed to Hg and fed ad libitum (Heinz, 1979). Alternatively, Hg 488 could increase energy storage by disrupting the metabolism of carbohydrates or lipids 489 [Seewagen (2020) and references therein]. However, in another experimental study, Hg-490 treated *Taeniopygia guttata* individuals waited longer to commence foraging and showed a 491 significant decrease in their body mass, after exposure to predation risk (Kobiela et al., 2015). 492 Other experimental studies showed no effect of Hg on body condition despite reduced 493 appetite, motivation to forage, and possibly low foraging efficiency (Bouton et al., 1999; 494 Spalding et al., 2000; Adams & Frederick, 2008). Overall, experimental studies point to 495 disruption of feeding behaviour, and/or nutrient and energy metabolism, with positive, 496 negative or no consequences on body condition. This suggests that metabolic effects of Hg 497 may be weak, and thus become (statistically) detectable only at high exposure levels, and/or 498 under specific conditions that could not be identified by the meta-analysis. Experimental data 499 sets were only eight in number and suffered from a slight publication bias. Therefore, we cannot exclude that further experimental work in a larger sample of individuals and species 500 501 could reveal a different picture.

502 Previous investigations and literature reviews highlighted substantial heterogeneity in 503 the strength and direction of the effect of Hg concentrations on body condition in wild birds: 504 studies reported significantly negative (e.g. Ackerman *et al.*, 2012, 2019; Fort *et al.*, 2015; 505 Adams *et al.*, 2020*a*), positive (e.g. Kalisińska *et al.*, 2010), or no associations (e.g. Heath & 506 Frederick, 2005; Herring *et al.*, 2014; Tartu *et al.*, 2015). This heterogeneity could stem from 507 the small statistical power of several ecotoxicological field investigations. Meta-analytical 508 approaches can overcome this drawback and provide higher precision in the estimation of

effect sizes (Koricheva *et al.*, 2013). However, our meta-analysis confirmed the lack of a clear
pattern. The correlative data set included a large number of effect sizes, with a balanced
distribution of modalities for most moderators, and a lack of bias, thus suggesting that the
output of this meta-analysis including both published and unpublished data is robust.
Interestingly, we detected a (publication) bias towards studies that show a negative effect of
Hg on body condition, while positive effects were more likely to remain unpublished (Table
S6).

516 Among the 15 tested moderators in correlative studies, only wintering status was identified as a driving factor of cross-study heterogeneity in results. Wintering birds were 517 518 more likely to show a negative effect of Hg concentrations on body condition, suggesting a 519 more detectable, negative effect when food is scarce and/or energetic demand for coping with 520 unfavourable weather conditions is high. This effect was driven by two studies on several 521 passerine species (Ackerman et al., 2012, 2019) and needs confirmation from other species. 522 As discussed above for metabolic and behavioural effects in experimental settings, food 523 intake and predation risk could be critical in driving effects of Hg concentration on body 524 condition. Feeding rates, food availability and predation risk are challenging to measure in the 525 wild, and could thus be key factors potentially confounding the Hg-body condition 526 association *in natura*. In conclusion, there is a need for further studies that measure Hg–body 527 condition associations while accounting for food intake and concurrent stressors (e.g. predation risk), especially at challenging life-cycle stages such as chick-rearing, migration, 528 529 overwintering and moult.

530

531 (2) Potential confounding factors and directions for future studies

Results from our meta-analysis indicate that body condition indices are not sensitive
endpoints of Hg sublethal effects in birds. In accordance with conclusions from Fuchsman *et*

534 al. (2017) and Evers (2018), reproductive endpoints should be preferred to estimate Hg 535 toxicity risk. Effects of Hg on reproductive success also have the advantage of being 536 comparable between laboratory-based and field studies in similar taxa (Evers, 2018). The 537 results of our meta-analysis also refute our prediction of smaller effect sizes of the Hg-body 538 condition association in piscivorous species, because of their naturally high Hg exposure over 539 evolutionary timescales (Scheuhammer et al., 2007; Evers, 2018). The lack of sensitivity of body condition indices to Hg effects could stem from several non-exclusive factors, some of 540 541 which are inherently linked to the concept of 'body condition'. Body condition indices have 542 been used as indicators of fat reserves, although not always explicitly so (reviewed in 543 Labocha & Hayes, 2012). However, body mass variation can be driven largely by lean mass, 544 not only fat mass, especially in migrating birds (Piersma, Gudmundsson & Lilliendahl, 1999; 545 Seewagen & Guglielmo, 2011). As such, body condition indices may be poor indicators of 546 energy stores in species with intrinsically low percentage of body lipids (Jacobs et al., 2012), 547 and be no more informative than body mass alone (Labocha & Hayes, 2012). Here, we found 548 no effect of body condition index type on the Hg-body condition association (Tables S2 and 549 S4). Previous studies have shown that it is complicated to draw generalisations on which body 550 condition index best represents body condition, but that different indices are often correlated 551 (Labocha et al., 2014; Kraft et al., 2019). We can speculate that if Hg had a clear impact on 552 body condition in birds, effects would be detected irrespective of the index used, but further studies are needed to address this point specifically. In addition, body condition indices can 553 554 vary substantially with season, sex and other factors, complicating comparisons among 555 studies (Labocha & Hayes, 2012; Labocha et al., 2014). For instance, effects of Hg on body 556 condition have been shown to depend on time of day in migrating passerines (Adams *et al.*, 557 2020b), as body mass can fluctuate strongly across the day in small birds. To investigate 558 further the potential role of energy storage and use on the relationship between Hg

559 concentration and body condition, we tested the effect of BM ratio and BMR as moderators. 560 The BM ratio is an indicator of maximum body condition and energy reserves (Vincze et al., 2019), while BMR represents the energy needed for basal body maintenance [in a resting, 561 562 post-absorptive phase, under thermoneutral conditions (McNab, 1997; Ellis & Gabrielsen, 563 2001; White et al., 2007)]. Both species-specific BM ratio and BMR were poor predictors of 564 the variation in the Hg-body condition association. However, only a third of the species 565 included in the analysis had known BMR information, and BMR also can vary depending on 566 other factors, such as temperature and latitude (Ellis & Gabrielsen, 2001; White et al., 2007), or the presence of other environmental contaminants such as persistent organic pollutants 567 568 (Blévin et al., 2017). The influence of energy storage strategies and BMR on the association 569 between Hg contamination and body condition needs further investigation, and likely works at 570 the individual level, which cannot be accounted for by meta-analytical approaches.

571 Physiological factors could also confound the relationship between Hg concentration and body condition in birds. An example of this is the potential mismatch between the 572 573 temporal integration of Hg into feathers and the timing of body condition measures (see also 574 Section II.1). In addition, the Hg-body condition relationship could reflect mechanisms for 575 dilution (or concentration) of Hg in tissues following body mass gain (or loss). However, this 576 has been shown only in two studies on healthy individuals [Hg dilution in blood in growing 577 juvenile birds (Ackerman, Eagles-Smith & Herzog, 2011); Hg concentration in blood in fasting passerines during simulated migratory fasting (Seewagen et al., 2016)], and in seabirds 578 579 that died from starvation (Fort et al., 2015). Further evidence from multiple avian species is 580 necessary to confirm whether adaptive changes in body mass and body mass composition, 581 which are necessary to sustain energy-demanding activities such as moulting, migrating and 582 breeding (Bech, Langseth & Gabrielsen, 1999), could drive variation in circulating Hg 583 concentrations. To this end, we encourage the use of other non-invasive indices of body

condition, such as pectoral muscle thickness (a proxy of lean mass; e.g. Sears, 1988), or body
composition assessed *via* quantitative magnetic resonance (Seewagen *et al.*, 2016; Ma *et al.*,
2018), and to account for sampling time of day (Adams *et al.*, 2020*b*).

587 Another possible factor confounding the Hg-body condition association could be 588 selenium (Se) status. Se can play a protective role against Hg toxicity at the biochemical level 589 (Cuvin-Aralar & Furness, 1991; Ralston, Blackwell & Raymond, 2007; Scheuhammer et al., 590 2015). The formation of apparently nontoxic Hg–Se granules observed in wildlife after MeHg 591 demethylation is considered the primary detoxification mechanism of MeHg, and enables long-term storage of Hg (Manceau et al., 2021). However, the mutual sequestration of Hg and 592 593 Se can be detrimental. Specifically, Hg can inhibit Se-dependent enzymes (selenoenzymes), 594 which are critical for brain health function, especially in early life (Ralston et al., 2008; 595 Ralston, Ralston & Raymond, 2016). Sublethal effects of Hg and the Hg-body condition 596 association could thus be influenced by the presence and bioavailability of Se in the diet, but 597 this is still understudied with respect to the toxic effects of Hg in avian species. Quantifying 598 the Se:Hg molar ratio (Scheuhammer et al., 2015), and/or a risk assessment criterion that 599 accounts for concurrent intake of MeHg and Se (Se health benefit value; Ralston et al., 2016), 600 could improve our understanding of the sublethal effects of Hg in birds.

601

602 V. CONCLUSIONS

603 (1) Our meta-analysis indicates that body condition is an unreliable endpoint of the sublethal604 effects of Hg in wild birds.

605 (2) Associations of Hg with body condition appear to be clearer under controlled conditions606 and further investigations are needed.

607 (3) Wintering birds were more likely to show a negative association between Hg and body608 condition in the wild, but further studies should confirm this in additional taxa.

609 (4) We highlight a substantial knowledge gap on the metabolic effects of Hg in waders and
610 raptors, birds in freshwater habitats and from tropical/subtropical regions, and especially in
611 migrating and overwintering birds.

612 (5) Our results indicate the need for further studies in both the laboratory and the field on the
613 effects of Hg on feeding rates, foraging efficiency, and energy storage and use in a larger
614 sample of individuals and species.

615

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- 1236
- 1237 VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information sectionat the end of the article.

- 1240 Table S1. Relevant studies that could not be included in the meta-analysis, with reasons for1241 exclusion.
- 1242 Table S2. Test of the effect of specific body condition types on the relationship between
- 1243 mercury (Hg) concentration and body condition in correlative studies, while accounting for
- 1244 random factors 'effect ID' and 'species ID'.
- 1245 Table S3. Akaike Information Criterion (AIC) selection for the best random structure of the1246 full model for moderator analyses.
- 1247 Table S4. AICc values of multifactorial models accounting for selected random factors (see
- 1248 Table S3) including the effect of age class, tissue and their interaction (Age class*Tissue)
- 1249 alone (base model) and with the addition of different moderators in the correlative data set.
- 1250 Table S5. Omnibus test results of single-predictor models to quantify the drivers of variation
- 1251 in the effect size of the association between Hg exposure and body condition in experimental
- 1252 studies in birds.
- 1253 Table S6. Funnel plots for published (left) and unpublished (right) correlative studies, where
- 1254 black dots indicate observed effect sizes and white open dots are imputed 'missing' effect
- 1255 sizes, based on the asymmetry of the funnel plot.

| Reference* | Year | Location | Species | ES | Tissue | Age class | Condition |
|--|------------|---------------------------------------|---------------------------|----------|-----------------|-----------|----------------|
| Completive station | | | | | | | type |
| Correlative studies | 2012 2012 | Control Volloy of Colifornia | 10 magazina anaziaa | 70 | Dlood & Foother | A duit | Dody condition |
| Ackerman <i>et al.</i> (2019) | 2012, 2013 | Central valley of California | 40 passerine species | /8 54 | Blood & Feather | Adult | Body condition |
| Adams <i>et al.</i> (2020 <i>a</i>) | 2013-2017 | Multiple sites in New York State, USA | 54 passerine species | 54 | Blood | Adult | Body condition |
| Adams <i>et al.</i> (2020 <i>b</i>) | 2009–2012 | Bill Baggs Cape Florida State Park | 8 passerine species | 12 | Blood | Adult | Body condition |
| Amélineau et al. (2019) | 2004–2015 | East Greenland | Alle alle | 1 | Feather | Adult | Body condition |
| Unpublished O.G., G.Y.* | 2018, 2019 | North-East Greenland | Pagophila eburnea | 2 | Blood | Adult | Body condition |
| Unpublished E.G.* | 2017, 2018 | Talan Island, Sea of Okhotsk, Russia | 2 seabird species | 2 | Feather | Adult | Body condition |
| Unpublished H.S.* | 2015-2018 | Bjornoya Island, Barents Sea, Norway | 4 seabird species | 7 | Blood & Feather | Adult | Body condition |
| Unpublished A.P.W., A.K.* | 2015, 2016 | Saint Lawrence Island, Bering Sea | 6 seabird species | 11 | Blood & Feather | Adult | Body condition |
| Carravieri et al. (2018) | 2011-2014 | Dronning Maud Land, Antarctica | Thalassoica antarctica | 2 | Blood | Adult | Body mass |
| Carravieri et al. (2020a) | 2018 | Isle of May, Firth of Forth, Scotland | Phalacrocorax aristotelis | 2 | Blood | Adult | Body condition |
| Eckbo et al. (2019) | 2015 | Svalbard, Norwegian Arctic | Cepphus grylle mandtii | 1 | Blood | Adult | Body condition |
| Unpublished J.F.* | 2019 | Tromelin & Ile dy Lys, Indian Ocean | 3 seabird species | 6 | Blood | Adult | Body condition |
| Gurney et al. (2014) | 2002, 2003 | Redberry Lake, Canada | Melanitta fusca | 1 | Blood | Adult | Body mass |
| Hargreaves et al. (2010, 2011) | 2009 | Southampton Island, Nunavut | 6 wader species | 7 | Blood | Adult | Body condition |
| Unpublished K.L.* | 2017 | Karrak Lake, Nunavut | 2 wader species | 2 | Blood | Adult | Body mass |
| Kojadinovic et al. (2007a) | 2004 | Multiple sites, Western Indian Ocean | Onychoprion fuscatus | 1 | Feather | Adult | Body mass |
| Provencher et al. (2016a) | 2013, 2014 | Mittivik Is, Northern Hudson Bay, | Somateria mollissima | 1 | Blood | Adult | Body condition |
| $\mathbf{D}_{\mathbf{r}} = \left(\frac{1}{2} \left(2014 \right) \right)$ | 2011 2012 | Canada | F | 1 | Dlaad | A .114 | Dedu eenditien |
| Rowse <i>et al.</i> (2014) | 2011, 2012 | Upper Sciolo River, Onio, USA | Emplaonax virescens | 1 | Blood | Adult | Body condition |
| Scheuhammer <i>et al.</i> (2016) | 2008 | Manitoba & Saskatchewan, Canada | Gavia immer | 4 | Blood & Feather | Adult | Body mass |
| Seewagen (2013) | 2008, 2009 | New York, USA | Parkesia noveboracensis | I | Blood | Adult | Body mass |
| Unpublished C.L.S.* | 2007, 2008 | New York, USA | Hylocichla mustelina | 1 | Blood | Adult | Body mass |
| Soldatini et al. (2020) | 2017 | Natividad Island, Mexico | Puffinus opisthomelas | 1 | Blood | Adult | Body condition |
| Tartu et al. (2013) | 2008, 2011 | Svalbard, Norwegian Arctic | Rissa tridactyla | 2 | Blood | Adult | Body condition |
| Tartu et al. (2014) | 2008 | Terre Adéie, Antarctica | Pagodroma nivea | 2 | Blood | Adult | Body condition |
| Tartu et al. (2015) | 2010 | Terre Adélie, Antarctica | Pagodroma nivea | 2 | Blood | Adult | Body condition |
| Tartu et al.(2016) | 2012, 2013 | Svalbard, Norwegian Arctic | Rissa tridactyla | 2 | Blood | Adult | Body condition |
| Albertos et al. (2020) | 2005-2020 | Alicante, Spain | 2 seabird species | 2 | Feather | Adult | Body mass |

Table 1. Studies included in the meta-analysis. Abbreviation: ES, number of effect sizes.

| Ackerman et al. (2012) | 2006–2010 | South San Francisco Bay, USA | Rallus longirostris obsoletus | 2 | Blood & Feather | Adult | Body condition |
|--|--|--|----------------------------------|----|-----------------|------------------|----------------|
| Wayland et al. (2001, 2002, 2003, 2005) | 1997, 1998 | East Bay Migratory Bird Sanctuary, Nunavut | Somateria mollissima | 1 | Blood | Adult | Body condition |
| Lerma <i>et al.</i> (2016) 2011, 2012 | | Bahia Santa Maria, Sinaloa, Mexico | Sula nebouxii | 3 | Blood | Adult & Chick | Body condition |
| Unpublished P.B., A.C., O.C., Y.C.* 2012 | | French Austral Territories, Southern 15 seabird species Ocean | | 52 | Blood & Feather | Adult & Chick | Body condition |
| Sebastiano et al. (2017) | 2013 | Grand Connetable, French Guyana | 6 seabird species | 11 | Blood | Adult & Chick | Body condition |
| Weech <i>et al.</i> (2006) | 2000–2002 | lakes, British Columbia | Haliaeetus leucocephalus | 2 | Blood | Adult & Chick | Body mass |
| Clarkson et al. (2012) | 2009, 2010 | Virginia and New York, USA | 1 seabird, 1 wader species | 2 | Feather | Chick | Body mass |
| Costantini et al. (2020) | 2016-2018 | Linosa, Italy | Calonectris diomedea | 2 | Blood | Chick | Body mass |
| Carravieri et al. (2020b) | Carravieri <i>et al.</i> (2020 <i>b</i>) 2012 | | 13 seabird species | 13 | Blood | Chick | Body condition |
| Unpublished P.B., J.F.* | 2015-2017 | French Coast, English Channel | 4 seabird species | 8 | Blood & Feather | Chick | Body condition |
| Carravieri et al. (2017) | 2012 | French Austral Territories, Southern Ocean | 2 seabird species | 3 | Blood | Chick | Body condition |
| Herring et al. (2014) | 2006, 2007 | Everglades, Florida | 2 wader species | 2 | Blood | Chick | Body condition |
| Kojadinovic <i>et al.</i> (2007 <i>b</i>) 2002–2004 | | Reunion Island, Western Indian Ocean | 2 seabird species | 2 | Feather | Chick | Body condition |
| Ortiz-Santaliestra <i>et al.</i> (2015) 2010, 2011 | | Castilla and Leon, Andalusia, Spain | Aquila fasciata | 4 | Blood | Chick | Body condition |
| Santos <i>et al.</i> (2017) 2012, 2013 | | Belgium | Larus fuscus | 1 | Feather | Chick | Body condition |
| Santos et al. (2020) | 2015 | Ostend, Belgium | Larus fuscus | 1 | Feather | Chick | Body mass |
| Experimental studies | | | | | | | |
| Seewagen et al. (2016); Gerson et al. (2019) | 2015 | Laboratory | Taeniopygia guttata | 4 | Blood | Adult | Body mass |
| Kobiela et al. (2015) | 2014 | Laboratory | Taeniopygia guttata | 2 | Blood | Adult | Body condition |
| Seewagen et al. (2019) | 2016-2017 | Long Point, Lake Erie, Canada | Setophaga coronata | 1 | Blood | Adult | Body condition |
| Ma et al. (2018) | 2014-2017 | Long Point, Lake Erie, Canada | Setophaga coronata | 4 | Blood | Adult | Body mass |
| Kenow et al. (2003) | 1999, 2000 | Laboratory | Gavia immer | 1 | Blood | Chick | Body condition |
| Fallacara et al. (2011) | 2005 | Laboratory | Falco sparverius | 2 | Blood | Chick | Body condition |
| Spalding et al. (2000) | 1996 | Everglades, Florida | Ardea alba | 2 | Blood | Chick | Body condition |
| Yu et al. (2016) | 2015 | Laboratory | Taeniopygia guttata | 4 | Blood | Chick | Body condition |

1257 * Authors involved in unpublished work, in alphabetical order: Paco Bustamante (P.B.), Alice Carravieri (A.C.), Olivier Chastel (O.C.), Yves Cherel (Y.C.), Jérôme Fort (J.F.), Olivier Gilg

1258 (O.G.), Elena Golubova (E.G.), Alexander Kitaysky (A.K.), Katelyn Luff (K.L.), Chad L. Seewagen (C.L.S.), Hallvard Strøm (H.S.), Alexis P. Will (A.P.W.), Glenn Yannic (G.Y.).

| Moderator | Modalities (number of effect sizes) ^a | Expected influence on the Hg-body condition association | | | | |
|-----------------------------------|--|--|--|--|--|--|
| | | | | | | |
| Bird type ^b | Passerine (145; 15), Raptor (6; 2), Seabird (150; 1), Wader (14; 2) | Physiological or life-history related differences in sensitivity to Hg | | | | |
| Age class | Adult (256; 11), Chick (59; 9) | Age-related sensitivity to Hg | | | | |
| Accounted for sex | Yes (18; 5), No (297; 15) | Sex-related sensitivity to Hg | | | | |
| Accounted for other variables | Yes (6; 11), No (309; 9) | Accounting for other confounding factors may modulate effect sizes | | | | |
| Dietary guild | Carnivore (114; 5), Herbivore (25; 10), Invertivore (143; 5), Omnivore (33; 0) | Potential exposure to different Hg chemical forms | | | | |
| Habitat type ^b | Freshwater (9; 1), Marine (153; 0), Terrestrial (153; 19) | Potential exposure to different Hg chemical forms | | | | |
| Zone ^b | Polar/subpolar (105; 0), Temperate (156; 18), Tropical/subtropical (54; 2) | Different energetic demands may change susceptibility to Hg | | | | |
| Wintering ^b | Yes (16; 0), No (299; 20) | | | | | |
| Migrating | Yes (41; 5), No (274; 15) | Physiological status, energetic demands and benaviour of different life- | | | | |
| Breeding ^b | Yes (197; 0), No (118; 20) | instory stages may change susceptionity to fig | | | | |
| Tissue ^b | Blood (213; 20), Feather (102; 0) | Tissue-specific temporal integration of Hg | | | | |
| Body condition index ^b | Body mass (19; 17), Size-corrected body mass (296; 3) | Index-associated influence on the Hg-body condition relationship | | | | |
| | | | | | | |
| Covariate | Unit (number of effect sizes) | | | | | |
| Hg concentration | μ g/g (315; 20) (dw and ww for correlative and experimental studies, respectively) | Concentration-dependent susceptibility to Hg | | | | |
| BMR | kJ/day (132; 17) | Energetic needs may influence the susceptibility to Hg | | | | |
| BM ratio | no unit (315; 20) | Potential effect of fat load on body condition | | | | |
| | | | | | | |

1259 Table 2. List of moderators included in the meta-analysis. Abbreviations: BM, body mass; BMR, basal metabolic rate; dw, dry mass; ww, wet mass. Hg-

^a The first and second number are for correlative and experimental studies, respectively.

^b Moderators not included in meta-analytic models of experimental studies given the limited sample size.

- **Fig. 1.** PRISMA[©] diagram describing the different phases of the systemic review on the
- 1263 association between Hg contamination and body condition, where *N* is the number of studies.
- 1264 *Some data sets were published in more than one scientific article, see Table 1.





Fig. 2. Funnel plot for correlative (left) and experimental (right) studies.

| 1270 | Fig. 3. Forest plot of the effect size for observed relationships between Hg concentrations and |
|------|---|
| 1271 | body condition in birds in correlative studies, depending on ecological, physiological and |
| 1272 | methodological factors (Fisher's Z scores [\pm 95% confidence interval]), while accounting for |
| 1273 | tissue type, age class and their interaction. The dashed line represents a null effect size |
| 1274 | (Fisher's $Z = 0$). Negative effect sizes indicate lower body condition with increased Hg |
| 1275 | concentrations. The size of the squares for the mean effect size is proportional to the number |
| 1276 | of observations the effect size estimate is based on. Individual effect size and study are |
| 1277 | random factors. Model estimates are considered statistically significant if their 95% |
| 1278 | confidence interval does not cross zero. Abbreviations: BM ratio, body mass ratio; BMR, |
| 1279 | basal metabolic rate; Body cond. index, body condition index; dw, dry mass; [Hg], Hg |
| 1280 | concentration; Other var. acc., other variables taken into account; ppm, parts per million; Sex |
| 1281 | acc., sex taken into account; Size-corr. body mass, size-corrected body mass. |

| | size | | interval | p-value | |
|---------------------------------------|------|----------------------|----------------|---------|----------|
| \ge class * Tissue + bird type | 315 | Passerine | [-0.082-0.033] | 0.406 | -8- |
| | | Raptor | [-0.284-0.252] | 0.907 | |
| | | Seabird | [-0.035-0.103] | 0.334 | |
| | | Wader | [-0.307-0.019] | 0.084 | |
| \ge class * Tissue + habitat type | 315 | Freshwater | [0.001-0.380] | 0.049 | |
| | | Marine | [-0.057-0.078] | 0.765 | |
| | | Terrestrial | [-0.087-0.024] | 0.261 | -8- |
| \ge class * Tissue + zone | 315 | Polar/subpolar | [-0.024-0.130] | 0.175 | |
| | | Temperate | [-0.088-0.024] | 0.266 | -8- |
| | | Tropical/subtropical | [-0.119-0.060] | 0.519 | |
| \ge class * Tissue + dietary guild | 315 | Carnivore | [-0.069-0.093] | 0.773 | |
| | | Herbivore | [-0.251-0.021] | 0.098 | |
| | | Invertivore | [-0.062-0.056] | 0.922 | |
| | | Omnivore | [-0.128-0.111] | 0.885 | _ |
| \ge class * Tissue + other var. acc. | 315 | No | [-0.054-0.042] | 0.805 | -8- |
| | | Yes | [-0.264-0.102] | 0.383 | |
| Age class * Tissue + sex acc. | 315 | No | [-0.059-0.039] | 0.698 | |
| - | | Yes | [-0.123-0.107] | 0.892 | |
| Age class * Tissue + body cond. index | 315 | Body mass | [-0.247-0.054] | 0.208 | |
| | | Size-corr. body mass | [-0.051-0.046] | 0.926 | -8- |
| \ge class * Tissue + BM ratio | 315 | BM ratio | [-0.344-0.202] | 0.609 | . |
| Age class * Tissue + migrating | 315 | No | [-0.050-0.048] | 0.968 | -8- |
| | | Yes | [-0.165-0.040] | 0.228 | |
| Age class * Tissue + breeding | 315 | No | [-0.163-0.018] | 0.105 | |
| | | Yes | [-0.044-0.055] | 0.835 | |
| Age class * Tissue + wintering | 315 | No | [-0.048-0.045] | 0.960 | -8- |
| - | | Yes | [-0.4060.025] | 0.027 | - |
| Age class * Tissue + log([Hg] ppm dw) | 315 | log([Hg] ppm dw) | [-0.028-0.035] | 0.809 | <u>_</u> |
| Age class * Tissue + log(BMR kJ/day) | 132 | log(BMR kJ/day) | [-0.044-0.024] | 0.560 | |

1284 Fig. 4. Forest plot of the effect size for observed relationships between Hg contamination and 1285 body condition in birds in experimental studies, depending on ecological, physiological and 1286 methodological factors (Fisher's Z scores [\pm 95% confidence interval]). The dashed line 1287 represents a null effect size (Fisher's Z = 0). Negative effect sizes indicate lower body 1288 condition with increased Hg exposure. The size of the squares for the mean effect size is 1289 proportional to the number of observations the effect size estimate is based on. Individual 1290 effect size and study are random factors. Model estimates are considered statistically 1291 significant if their 95% confidence interval does not cross zero. Abbreviations: BM ratio, 1292 body mass ratio; BMR, basal metabolic rate; [Hg], Hg concentration; Other var. acc., other 1293 variables taken into account; ppm, parts per million; Sex acc., sex taken into account; ww, wet

1294 mass.

| Explanatory | Sample size | Level | 95% confidence interval | p–value | |
|------------------|----------------|------------------|----------------------------|---------|-----|
| log([Hg] ppm dw) | 20 | log([Hg] ppm dw) | [-0.253-0.225] | 0.905 | -8- |
| Dietary guild | 20 | Carnivore | [-1.951–0.629] | 0.295 | |
| | | Herbivore | [-0.119–1.688] | 0.065 | |
| | | Invertivore | [-1.169–1.410] | 0.846 | |
| Other var. acc. | 20 | No | [-0.336–1.644] | 0.182 | |
| | | Yes | [-0.950-0.834] | 0.893 | |
| Sex acc. | 20 | No | [-0.360–1.192] | 0.275 | |
| | | Yes | [-1.566–1.142] | 0.746 | |
| Age class | 20 | Adult | [-0.036–1.636] | 0.060 | |
| | | Chick | [-1.313-0.532] | 0.386 | |
| Migrating | | No | [-0.863–1.321] | 0.665 | |
| | | Yes | [-1.615–2.277] | 0.725 | |
| BM ratio | 20 | BM ratio | [-0.301–0.740] | 0.389 | |
| log(BMR kJ/day) | 20 | log(BMR kJ/day) | [-0.059–0.400] | 0.136 | |

1295

-2 -1.5 -1 -0.5 0 0.5 1 1.5 2 2.5 Effect of mercury on body condition