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

Alice Carravieri, Orsolya Vincze, Paco Bustamante, Joshua Ackerman, Evan Adams, Frédéric Angelier, Olivier Chastel, Yves Cherel, Olivier Gilg, Elena Golubova, et al.

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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  
64 influence of intrinsic, extrinsic and methodological factors potentially explaining cross-study  
65 heterogeneity in results. We considered experimental and correlative studies carried out in  
66 adult birds and chicks, and mercury exposure inferred from blood and feathers. Most  
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  $0.262 \pm 0.309$ , 20 effect sizes, five species) and correlative studies ( $-0.011 \pm 0.020$ , 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  
86 mercury further using designs that allow for the estimation and/or manipulation of food intake

87	in both wild and captive birds, especially in under-represented life-history stages such as
88	migration and overwintering.
89	
90	<i>Key words:</i> blood, body mass, fat, feather, feeding, energetics, habitat, metabolism, species.
91	
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## 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  
128 concentrations (Walker *et al.*, 2012; UN Environment, 2019). In its inorganic form, Hg has an  
129 atmospheric lifetime of 0.5–1 year and can be transported over vast spatial scales (Obrist *et al.*,  
130 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  
147 immune disruption with consequences on development, neurocognitive function, and  
148 reproduction (Tchounwou *et al.*, 2003; Heinz *et al.*, 2009; Tan, Meiller & Mahaffey, 2009;  
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;  
153 Polito *et al.*, 2016; Ma *et al.*, 2021) but other traits such as sex and age can also modulate this  
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  
157 variation in Hg burdens (Seewagen, Cristol & Gerson, 2016; Ackerman, Hartman & Herzog,  
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; Martinson, Marcogliese & Verreault, 2017;



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

169         Here, we performed a meta-analysis investigating the effect of Hg contamination on  
170 body condition using information extracted from 47 studies on 147 species of birds. Body  
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)  
178 and/or physiology (e.g. disruption of nutrient metabolism and energy use). We chose birds as  
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  
198 (Robinson *et al.*, 2011; Manceau *et al.*, 2021)]. Piscivorous species might therefore show a  
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)  
204 across all years, using the search terms “mercury”, “bird” and “body condition”. Since body  
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  
207 “mercury”, “bird” and one of the following key words: “effect”, “health”, “telomere”,  
208 “oxidative stress”, “hormone”, “corticosterone”, “testosterone”, “thyroid”, “immunity”,  
209 “parasite”, “DNA damage”, “energy”, “hatching/fledging/breeding success”, “hatch date”,  
210 “clutch size”, “foraging behaviour”, “survival”, “growth” and “body mass”. The reference  
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

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

$$240 \quad \dot{M}_i = M_i L_0^{b_{\text{SMA}}}/L_i$$

241 where  $M_i$  and  $L_i$  are the body mass and the body length measure of individual  $i$ , respectively;  
242 the exponent  $b_{\text{SMA}}$  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

256 The form of Hg in avian diets may vary depending on prey types. High-trophic-level  
257 prey, such as fish and squid, mainly contain Hg as MeHg, whereas invertebrates may have  
258 higher proportions of inorganic Hg (Bloom, 1992; Mason, Laporte & Andres, 2000;  
259 Bustamante *et al.*, 2006; Seco *et al.*, 2020). All included studies measured total Hg, which is  
260 an accurate proxy of MeHg in tissues such as blood and feathers (e.g. Bond & Diamond,  
261 2009; Renedo *et al.*, 2021).

262

263 (c) *Exposure pathway and measure*

264 We included experimental studies where adults and chicks were exposed to Hg *via*  
265 dietary exposure as MeHg, as well as MeHg egg injections. We considered studies where Hg  
266 contamination was inferred from concentrations [in parts per million (ppm) or  $\mu\text{g}$  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,

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

288

289 *(d) Other criteria*

290 Studies comparing body condition indices between populations at polluted sites where  
291 pollution was not clearly Hg-related were also excluded, as well as studies on dead, emaciated  
292 individuals (Table S1), where body condition could be biased. Effect sizes obtained from less  
293 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,  
297 raptor, seabird, wader); (2) age class (chick, adult); (3) whether the effect size had been  
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  $t$ -  
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 *et al.* (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 *et al.* (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**

334         In a preliminary step, we conducted a meta-analysis on the full data set including 335  
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-  
338 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  
344 regression tests (Egger *et al.*, 1997) using overall intercept-only models with the *regtest*  
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*

358 All meta-analytic models were performed using the *rma.mv* function in the *metafor*  
359 package (v. 2.4-0; Viechtbauer, 2010) in R (v. 4.0.5; R Core Team, 2021). We constructed  
360 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  
363 originating from the same studies, non-independence of observations of the same species, as  
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  
369 matrix representing the phylogenetic history of the species. For the latter, we used a rooted  
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  
383 ( $I^2_{\text{total}}$ ) based on an intercept-only meta-analytic model (built using the *rma* function in  
384 *metafor*), without any random effects.  $I^2$  represents the percentage heterogeneity in the effect  
385 sizes (0–100%) due to true heterogeneity rather than random sampling variance (Higgins &

386 Thompson, 2002; Higgins *et al.*, 2003).  $I^2$  was moderate to high (defined as  $I^2 > 50\%$ ; Higgins  
387 *et al.*, 2003, see Section III), therefore we ran moderator analyses to explore which life-  
388 history, ecological or physiological parameters could explain the high heterogeneity observed  
389 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 ~ 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  
402 considered, but data were too scarce to enable inclusion in the final meta-analysis. The  
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.

410 The experimental data set was too small for multifactorial statistical analysis ( $N = 20$   
411 effect sizes). Therefore, each moderator was entered as a single predictor to an intercept-only  
412 multilevel meta-analytic model (fitted by REML) with the selected random structure (Table  
413 S5). Using these models, we obtained parameter estimates for each predictor and factor level.  
414 The overall significance of each predictor was assessed using an omnibus test (Viechtbauer,  
415 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**

433 We used 315 population-specific effect sizes from 145 species to test the relationship  
434 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  
437 individuals inspected per effect size was 16 (range: 4–1051). Comparison of intercept-only  
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 =  $-0.011 \pm 0.020$ , confidence interval, CI  
443  $[-0.049; 0.027]$ , while accounting for individual effect size ID and species ID). Effect size  
444 heterogeneity was moderate ( $I^2 = 55\%$ ; Cochran's  $Q$  test = 668, df = 314,  $P < 0.0001$ ),  
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**

452 Experimental studies encompassed 20 effect sizes from five species (*Ardea alba*,  
453 *Falco sparverius*, *Gavia immer*, *Setophaga coronata*, *Taeniopygia guttata*). The median  
454 number of individuals inspected per effect size was 24 (range: 5–49). Only individual effect  
455 size ID was retained in the random structure of intercept-only multilevel meta-analytic models  
456 (Table S3). Hg contamination was not related to body condition ( $0.262 \pm 0.309$ ,  $[-0.344;$   
457  $0.867]$ , while accounting for individual effect size ID), and effect size heterogeneity was very  
458 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  
467 that waders and raptors, birds in freshwater habitats and tropical/subtropical regions, and  
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 &  
475 Swaddle, 2015; Yu *et al.*, 2016; Ma *et al.*, 2018). Therefore, the difference in sensitivity to  
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**

480         Accumulation of energy stores can be part of the response to stressors, whereby  
481 perceived risk or unpredictable access to food can cause birds to store energy as a buffer  
482 against unpredictable environmental changes [Schultner *et al.* (2013) and references therein].  
483 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  
486 increase in energy stores was likely linked to an increase in food intake, as shown in mallard  
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  
500 cannot exclude that further experimental work in a larger sample of individuals and species  
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.*, 2020a), 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

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

516         Among the 15 tested moderators in correlative studies, only wintering status was  
517 identified as a driving factor of cross-study heterogeneity in results. Wintering birds were  
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.  
528 predation risk), especially at challenging life-cycle stages such as chick-rearing, migration,  
529 overwintering and moult.

530

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

532         Results from our meta-analysis indicate that body condition indices are not sensitive  
533 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  
540 body condition indices to Hg effects could stem from several non-exclusive factors, some of  
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  
553 studies are needed to address this point specifically. In addition, body condition indices can  
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.*,  
561 2019), while BMR represents the energy needed for basal body maintenance [in a resting,  
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),  
567 or the presence of other environmental contaminants such as persistent organic pollutants  
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  
572 and body condition in birds. An example of this is the potential mismatch between the  
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  
578 fasting passerines during simulated migratory fasting (Seewagen *et al.*, 2016)], and in seabirds  
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

584 condition, such as pectoral muscle thickness (a proxy of lean mass; e.g. Sears, 1988), or body  
585 composition assessed *via* quantitative magnetic resonance (Seewagen *et al.*, 2016; Ma *et al.*,  
586 2018), and to account for sampling time of day (Adams *et al.*, 2020b).

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  
592 long-term storage of Hg (Manceau *et al.*, 2021). However, the mutual sequestration of Hg and  
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 sublethal  
604 effects of Hg in wild birds.

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

607 (3) Wintering birds were more likely to show a negative association between Hg and body  
608 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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652

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1236

## 1237 **VIII. SUPPORTING INFORMATION**

1238 Additional supporting information may be found online in the Supporting Information section  
1239 at the end of the article.

1240 **Table S1.** Relevant studies that could not be included in the meta-analysis, with reasons for  
1241 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 the  
1246 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.

1256 Table 1. Studies included in the meta-analysis. Abbreviation: ES, number of effect sizes.

Reference*	Year	Location	Species	ES	Tissue	Age class	Condition type
<i>Correlative studies</i>							
Ackerman <i>et al.</i> (2019)	2012, 2013	Central Valley of California	40 passerine species	78	Blood & Feather	Adult	Body condition
Adams <i>et al.</i> (2020a)	2013–2017	Multiple sites in New York State, USA	54 passerine species	54	Blood	Adult	Body condition
Adams <i>et al.</i> (2020b)	2009–2012	Bill Baggs Cape Florida State Park	8 passerine species	12	Blood	Adult	Body condition
Amélineau <i>et al.</i> (2019)	2004–2015	East Greenland	<i>Alle alle</i>	1	Feather	Adult	Body condition
Unpublished O.G., G.Y.*	2018, 2019	North-East Greenland	<i>Pagophila eburnea</i>	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 <i>et al.</i> (2018)	2011–2014	Dronning Maud Land, Antarctica	<i>Thalassoica antarctica</i>	2	Blood	Adult	Body mass
Carravieri <i>et al.</i> (2020a)	2018	Isle of May, Firth of Forth, Scotland	<i>Phalacrocorax aristotelis</i>	2	Blood	Adult	Body condition
Eckbo <i>et al.</i> (2019)	2015	Svalbard, Norwegian Arctic	<i>Cephus grylle mandtii</i>	1	Blood	Adult	Body condition
Unpublished J.F.*	2019	Tromelin & Ile dy Lys, Indian Ocean	3 seabird species	6	Blood	Adult	Body condition
Gurney <i>et al.</i> (2014)	2002, 2003	Redberry Lake, Canada	<i>Melanitta fusca</i>	1	Blood	Adult	Body mass
Hargreaves <i>et al.</i> (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 <i>et al.</i> (2007a)	2004	Multiple sites, Western Indian Ocean	<i>Onychoprion fuscatus</i>	1	Feather	Adult	Body mass
Provencher <i>et al.</i> (2016a)	2013, 2014	Mittivik Is, Northern Hudson Bay, Canada	<i>Somateria mollissima</i>	1	Blood	Adult	Body condition
Rowse <i>et al.</i> (2014)	2011, 2012	Upper Scioto River, Ohio, USA	<i>Empidonax virescens</i>	1	Blood	Adult	Body condition
Scheuhammer <i>et al.</i> (2016)	2008	Manitoba & Saskatchewan, Canada	<i>Gavia immer</i>	4	Blood & Feather	Adult	Body mass
Seewagen (2013)	2008, 2009	New York, USA	<i>Parkesia noveboracensis</i>	1	Blood	Adult	Body mass
Unpublished C.L.S.*	2007, 2008	New York, USA	<i>Hylocichla mustelina</i>	1	Blood	Adult	Body mass
Soldatini <i>et al.</i> (2020)	2017	Natividad Island, Mexico	<i>Puffinus opisthomelas</i>	1	Blood	Adult	Body condition
Tartu <i>et al.</i> (2013)	2008, 2011	Svalbard, Norwegian Arctic	<i>Rissa tridactyla</i>	2	Blood	Adult	Body condition
Tartu <i>et al.</i> (2014)	2008	Terre Adéie, Antarctica	<i>Pagodroma nivea</i>	2	Blood	Adult	Body condition
Tartu <i>et al.</i> (2015)	2010	Terre Adélie, Antarctica	<i>Pagodroma nivea</i>	2	Blood	Adult	Body condition
Tartu <i>et al.</i> (2016)	2012, 2013	Svalbard, Norwegian Arctic	<i>Rissa tridactyla</i>	2	Blood	Adult	Body condition
Albertos <i>et al.</i> (2020)	2005–2020	Alicante, Spain	2 seabird species	2	Feather	Adult	Body mass

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

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–

<b>Moderator</b>	<b>Modalities (number of effect sizes)<sup>a</sup></b>	<b>Expected influence on the Hg–body condition association</b>
Bird type <sup>b</sup>	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 <sup>b</sup>	Freshwater (9; 1), Marine (153; 0), Terrestrial (153; 19)	Potential exposure to different Hg chemical forms
Zone <sup>b</sup>	Polar/subpolar (105; 0), Temperate (156; 18), Tropical/subtropical (54; 2)	Different energetic demands may change susceptibility to Hg
Wintering <sup>b</sup>	Yes (16; 0), No (299; 20)	Physiological status, energetic demands and behaviour of different life-history stages may change susceptibility to Hg
Migrating	Yes (41; 5), No (274; 15)	
Breeding <sup>b</sup>	Yes (197; 0), No (118; 20)	
Tissue <sup>b</sup>	Blood (213; 20), Feather (102; 0)	Tissue-specific temporal integration of Hg
Body condition index <sup>b</sup>	Body mass (19; 17), Size-corrected body mass (296; 3)	Index-associated influence on the Hg–body condition relationship
<b>Covariate</b>	<b>Unit (number of effect sizes)</b>	
Hg concentration	µg/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

1260 <sup>a</sup> The first and second number are for correlative and experimental studies, respectively.

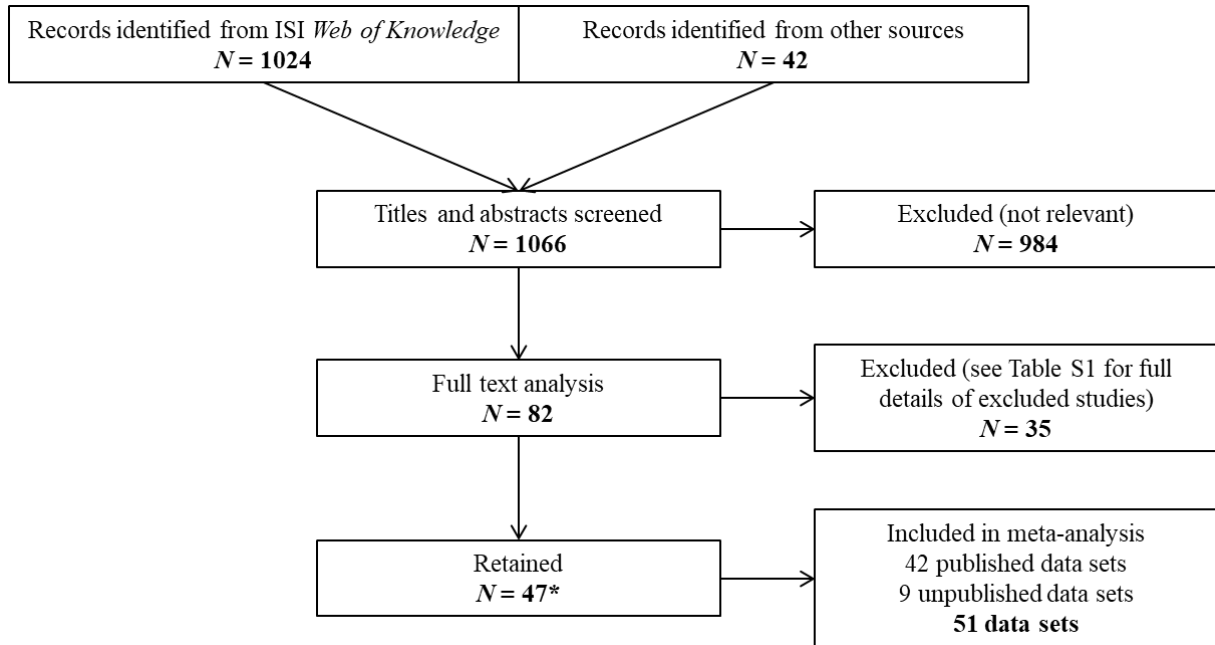
1261 <sup>b</sup> Moderators not included in meta-analytic models of experimental studies given the limited sample size.



1262 **Fig. 1.** PRISMA<sup>®</sup> 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.

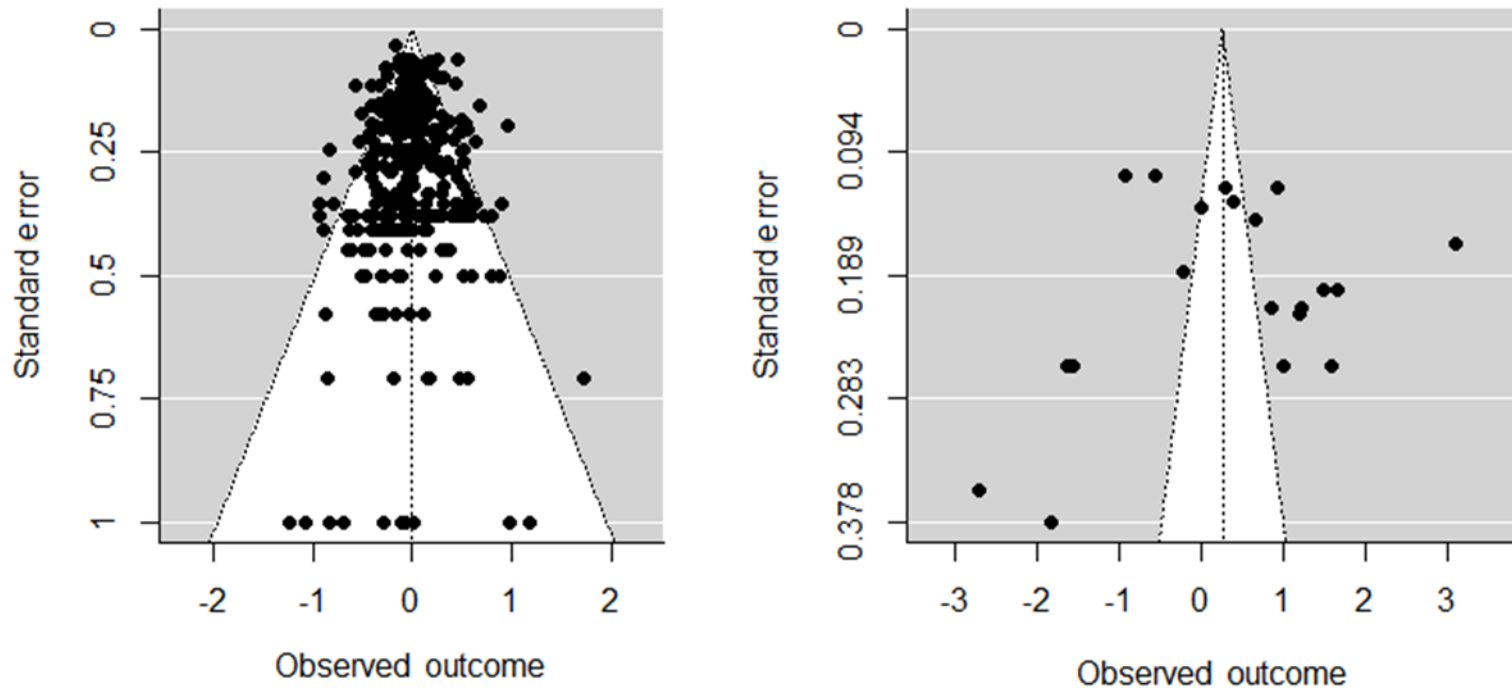
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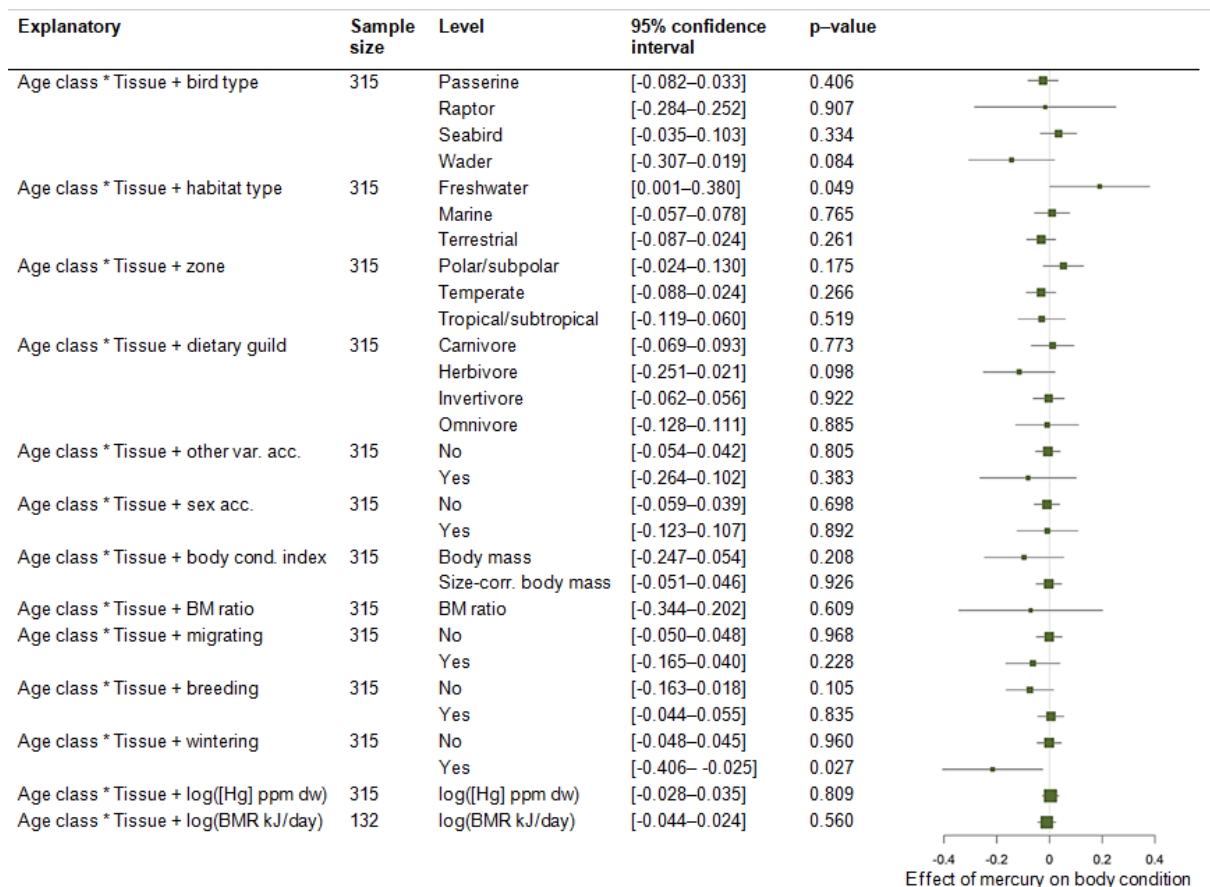
1267 **Fig. 2.** Funnel plot for correlative (left) and experimental (right) studies.

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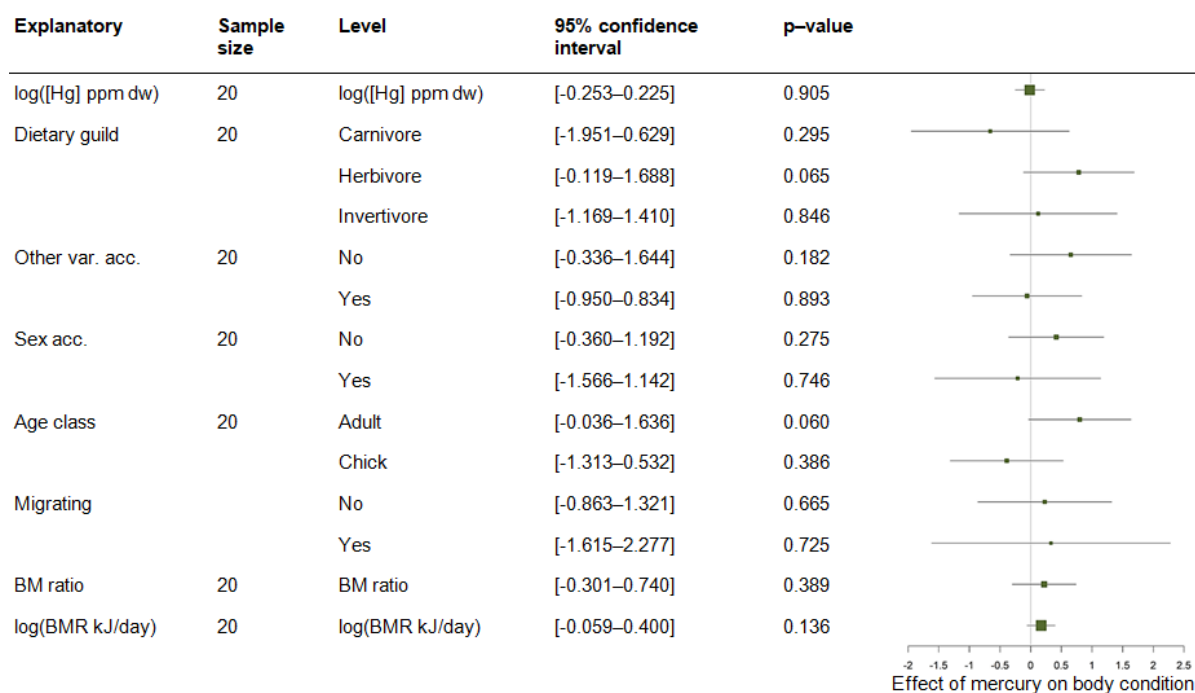
1270 **Fig. 3.** Forest plot of the effect size for observed relationships between Hg concentrations and  
1271 body condition in birds in correlative studies, depending on ecological, physiological and  
1272 methodological factors (Fisher's Z scores [ $\pm$  95% confidence interval]), while accounting 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.



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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.



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