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

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ABSTRACT

Mercury contamination is a major threat to the global environment, and is still increasing in some regions despite international regulations. The methylated form of mercury is hazardous to biota, yet its sublethal effects are difficult to detect in wildlife. Body condition can vary in response to stressors, but previous studies have shown mixed effects of mercury on body condition in wildlife. Using birds as study organisms, we provide the first quantitative 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 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 experimental

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investigations (90%) showed a significant relationship between mercury concentrations and body condition. Experimental exposure to mercury disrupted nutrient (fat) metabolism, metabolic rates, and food intake, resulting in either positive or negative associations with body condition. Correlative studies also showed either positive or negative associations, of which only 14% were statistically significant. Therefore, the overall effect of mercury concentrations on body condition was null in both experimental (estimate ± SE = 0.262 ± 0.309, 20 effect sizes, five species) and correlative studies (−0.011 ± 0.020, 315 effect sizes, 145 species). The single and interactive effects of age class and tissue type were accounted for in meta-analytic models of the correlative data set, since chicks and adults, as well as blood and feathers, are known to behave differently in terms of mercury accumulation and health effects. Of the 15 moderators tested, only wintering status explained cross-study heterogeneity in the correlative data set: free-ranging wintering birds were more likely to show a negative association between mercury and body condition. However, wintering effect sizes were limited to passerines, further studies should thus confirm this trend in other taxa. Collectively, our results suggest that (*i*) effects of mercury on body condition are weak and mostly detectable under controlled conditions, and (*ii*) body condition indices are unreliable indicators of mercury sublethal effects in the wild. Food availability, feeding rates and other sources of variation that are challenging to quantify likely confound the association between 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 in both wild and captive birds, especially in under-represented life-history stages such as migration and overwintering.

Key words: blood, body mass, fat, feather, feeding, energetics, habitat, metabolism, species

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I INTRODUCTION

Chemical pollution is a major anthropogenic modification of the global environment, and a fundamental characteristic of the Anthropocene (Lewis & Maslin, 2015). Humans are responsible for the synthesis and release of a plethora of chemical contaminants for agricultural uses [e.g. organochlorine and organophosphate pesticides (Jones & De Voogt, 1999; Sánchez-Santed, Colomina & Herrero Hernández, 2016)], and industrial or every-day life applications [e.g. metallic trace elements, perfluoroalkyl substances, chlorinated paraffins (Walker *et al.*, 2012; Sunderland *et al.*, 2019; Vorkamp *et al.*, 2019)]. Among these contaminants, and despite being a natural element, mercury (Hg) is particularly hazardous to 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 atmospheric lifetime of 0.5–1 year and can be transported over vast spatial scales

(Obrist *et al.*, 2018; UN Environment, 2019). Once deposited on the Earth's surface, Hg can undergo complex, microbially mediated processes and be converted into methylmercury (MeHg), which is assimilated and accumulated by living organisms, and biomagnifies in food webs (Atwell, Hobson & Welch, 1998; Evers *et al.*, 2016; Eagles-Smith *et al.*, 2018).

Anthropogenic Hg emissions have declined in North America and Europe over the past two decades (UN Environment, 2019), but are still increasing in East Asia and in the Southern Hemisphere (Obrist *et al.*, 2018). In addition, concentrations measured in wildlife are still increasing in several regions of the Northern (Braune *et al.*, 2014; Wang *et al.*, 2019) and Southern Hemispheres (Mills *et al.*, 2020; Seco *et al.*, 2020). The Minamata Convention, an international treaty that came into force in 2017 (http://www.mercuryconvention.org), adopted a global strategy to reduce Hg emissions and protect human and environmental health. While these global restrictions may limit increases in future Hg emissions linked to economic growth, legacy Hg emissions will continue to affect the Hg cycle for decades to centuries (Eagles-Smith *et al.*, 2018). Monitoring Hg concentrations and effects in biota and the environment is thus a priority to oversee the effectiveness of the Minamata Convention (Evers *et al.*, 2016).

Adverse effects of Hg in humans and wildlife include neurological, endocrine, and immune disruption with consequences on development, neurocognitive function, and reproduction (Tchounwou *et al.*, 2003; Heinz *et al.*, 2009; Tan, Meiller & Mahaffey, 2009; Tartu *et al.*, 2013; Goutte *et al.*, 2014; Eagles-Smith *et al.*, 2018; Evers, 2018). Several intrinsic and extrinsic factors drive variation in Hg contamination and kinetics in wild organisms. Feeding ecology is a key explanatory factor of among- and within-species 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 variation (Eagles-Smith *et al.*, 2009; Robinson, Lajeunesse & Forbes, 2012; Jackson *et al.*, 2015; Chételat *et al.*, 2020). In addition, life-history traits such as breeding or migration strategies can influence diet, feeding rate, energy storage and expenditure, thus driving variation in Hg burdens (Seewagen, Cristol & Gerson, 2016; Ackerman, Hartman & Herzog, 2019; Adams *et al.*, 2020a). All these intrinsic and extrinsic factors thus have the potential to modulate Hg toxicity. However, identifying sublethal effects of Hg in the field can be challenging, due to the potentially confounding influence of concurring environmental 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.

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 condition indices are available in a large number of studies and species, and they can be calculated from morphometric measures that are used routinely in avian investigations. Albeit widely used, body condition indices may not be reliable indicators of health status (Fischer, Taborsky & Dieckmann, 2009; Schultner *et al.*, 2013). Here, we consider body condition as an integrative measure of fat and lean mass (Peig & Green, 2009; Labocha & Hayes, 2012) that can be affected linearly or non-linearly by stressors (Pravosudov & Grubb, 1997; 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 the study taxon because they have served widely as early sentinels of negative effects of Hg on wildlife and ecosystem health (Wolfe, Schwarzbach & Sulaiman, 1998; Whitney & Cristol, 2018). Birds are ubiquitous, being found in a large variety of terrestrial, freshwater and marine habitats from polar regions to the tropics. In addition, they belong to different dietary guilds, from herbivores to omnivores, are relatively accessible compared to other groups of vertebrates, and are thus extensively studied (Konishi *et al.*, 1989). Our aim was twofold: (*i*) to test for a systematic trend in the effect of Hg on body condition in birds; and (*ii*) to identify moderators of this relationship among intrinsic (e.g. species, age class, sex) and extrinsic factors (habitat type, dietary guild), as well as methodological aspects (tissue used to measure Hg concentrations, correlative or experimental approach). As Hg can affect bird behaviour [e.g. reduced ability to forage and/or compete for food (e.g. Evers *et al.*, 2008)], metabolic rates (Gerson, Cristol & Seewagen, 2019), and physiological pathways involved in the stress response (Wada *et al.*, 2009; Franceschini *et al.*, 2017), which can have a range of contrasting consequences for physical condition, we expected either a positive or negative relationship between Hg concentrations and body condition. Given Hg biomagnification and naturally high bioavailability in aquatic environments (Atwell *et al.*, 1998; Fitzgerald, Lamborg & Hammerschmidt, 2007), piscivorous species can be at greater risk of Hg exposure (Scheuhammer *et al.*, 2007), and are thought to have developed a better tolerance to toxicity over evolutionary timescales [e.g. through more efficient detoxification mechanisms (Robinson *et al.*, 2011; Manceau *et al.*, 2021)]. Piscivorous species might therefore show a smaller effect size of the Hg–body condition association.

II MATERIALS AND METHODS

(1) Search and inclusion criteria

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 condition is often calculated in studies of the effect of Hg on physiological and fitness endpoints without being the

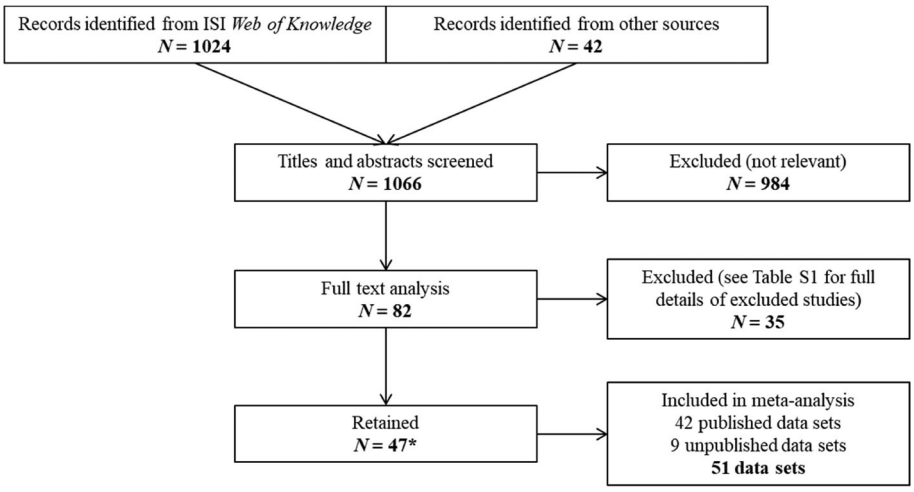

Fig. 1. PRISMA© diagram describing the different phases of the systemic review on the association between Hg contamination and body condition, where *N* is the number of studies. *Some data sets were published in more than one scientific article, see Table 1.

primary objective, we also searched the literature using the terms "mercury", "bird" and one of the following key words: "effect", "health", "telomere", "oxidative stress", "hormone", "corticosterone", "testosterone", "thyroid", "immunity", "parasite", "DNA damage", "energy", "hatching/fledging/breeding success", "hatch date", "clutch size", "foraging behaviour", "survival", "growth" and "body mass". The reference lists of literature reviews found in this way were also checked to expand the database (Fig. 1). We contacted the authors of studies to obtain further details when (*i*) statistical information was missing, and/or (*ii*) the effect size was calculated across several species. Incomplete statistical information and a lack of a response by contacted authors meant that some relevant studies had to be discarded (see online Supporting Information, Table S1). The literature search resulted in the selection of 47 studies spanning publication years 2000 to 2020 (Table 1). These covered data mainly on passerines and seabirds with a few waders and raptors (Table 1). In addition, we included nine studies from the authors' unpublished work in order to reduce the bias towards passerine birds. Overall, our meta-analysis included 147 species of birds, which were mainly passerines and seabirds. Inclusion criteria are detailed below.

(*a*) *Body condition indices*

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

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

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

Table 1. Studies included in the meta-analysis

Reference*	Year	Location	Species	ES	Tissue	Age class	Condition type
Correlative studies							
Ackerman *et al.* (2019)	2012, 2013	Central Valley of California	40 passerine species	78	Blood & Feather	Adult	Body condition
Adams *et al.* (2020a)	2013–2017	Multiple sites in New York State, USA	54 passerine species	54	Blood	Adult	Body condition
Adams *et al.* (2020b)	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, Canada	*Somateria mollissima*	1	Blood	Adult	Body condition
Rowse *et al.* (2014)	2011, 2012	Upper Scioto River, Ohio, USA	*Empidonax virescens*	1	Blood	Adult	Body condition
Scheuhammer *et al.* (2016)	2008	Manitoba & Saskatchewan, Canada	*Gavia immer*	4	Blood & Feather	Adult	Body mass
Seewagen (2013)	2008, 2009	New York, USA	*Parkesia noveboracensis*	1	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	

Table 1. *(Cont.)*

Reference*	Year	Location	Species	ES	Tissue	Age class	Condition type
							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
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 *et al.* (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 Ocean	15 seabird species	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 *et al.* (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)	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 *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 *et al.* (2007b)	2002–2004	Reunion Island, Western Indian Ocean	2 seabird species	2	Feather	Chick	Body condition
Ortiz-Santaliestra *et al.* (2015)	2010, 2011	Castilla and Leon, Andalusia, Spain	*Aquila fasciata*	4	Blood	Chick	Body condition
Santos *et al.* (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

(Continues)

Table 1. *(Cont.)*

Reference*	Year	Location	Species	ES	Tissue	Age class	Condition type
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

ES, number of effect sizes.
*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 (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.).

(*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).

(*c*) *Exposure pathway and measure*

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

(*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.

(2) Moderators included and categorisation

Our meta-analysis included a maximum of 15 moderators: (*i*) bird type (passerine, raptor, seabird, wader); (*ii*) age class (chick, adult); (*iii*) whether the effect size had been corrected for sex; (*iv*) whether the effect size had been corrected for other factors that were specific to the study (e.g. individual random factor, sampling date, season); (*v*) dietary guild (carnivore, herbivore, invertivore, omnivore); (*vi*) habitat type (freshwater, marine, terrestrial); (*vii*) geographical zone (polar/subpolar, temperate, tropical/subtropical); whether the sampled population was (*viii*) wintering (yes/no), (*ix*) migrating (yes/no) or (*x*) breeding (yes/no); (*xi*) tissue type used for Hg quantification (blood, feather); (*xii*) body condition index (body mass, size-corrected body mass); (*xiii*) species-specific basal metabolic rate (BMR); (*xiv*) Hg concentration; (*xv*) ratio of species-specific maximum body mass to average body mass (hereafter BM ratio, which reflects the maximum body condition of the species; Vincze *et al.*, 2019). All moderators, their modalities, the number of effect sizes, and the justification for including them to study the link between Hg concentration and body condition are reported in Table 2. Dietary guild was assigned based on results in the sampled population of each study when available, or from the Wilman *et al.* (2014) database. Species-specific BMR values were extracted from Ellis & Gabrielsen (2001), Møller (2009), Londoño *et al.* (2015) and McKechnie, Noakes & Smit (2015), but were not available for all species. Body mass information to calculate the BM ratio was extracted from the Dunning (2007) database, or from additional references (Glahn & McCoy, 1995; Shirihai *et al.*, 2002; Kooyman *et al.*, 2004; Helseth, Stervander & Waldenström, 2005; Tobón & Osorno, 2006; Kojadinovic *et al.*, 2007a; Overton *et al.*, 2009; Hancock, Kushlan & Kahl, 1992; Rising, 2010; García, Moreno-Opo & Tintó, 2013; Maccarone & Brzorad, 2016; studies included in the meta-analysis). For each study, we extracted the moderators, as well as sample and effect sizes as detailed below.

(3) Effect size extraction or calculation

Given that most studies were correlative, we chose Pearson's *r* as the effect size. Based on the information given in correlative studies, we calculated effect sizes using *t*-values, *F*-values, *P*-values, means and standard deviations, or correlation coefficients, following formulae given in Koricheva, Gurevitch & Mengersen (2013). For studies reporting the comparison of experimental groups, we calculated standardised mean differences (Cohen's *d*), which were then transformed to Pearson's *r*, following Koricheva *et al.* (2013). To adhere to normality assumptions, Pearson's *r* were then converted to Fisher's Zr following the equation in Lipsey & Wilson (2001). Sampling variances associated Z-scores were calculated as $(n–3)^{-1}$ following Koricheva *et al.* (2013). Positive effect sizes indicate a positive effect of Hg on body condition, while negative effect sizes denote a decrease in body condition with increasing Hg concentrations.

Table 2. List of moderators included in the meta-analysis

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)	Physiological status, energetic demands and behaviour of different life-history stages may change susceptibility to Hg
Migrating	Yes (41; 5), No (274; 15)	
Breeding[b]	Yes (197; 0), No (118; 20)	
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	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

BM, body mass; BMR, basal metabolic rate; dw, dry mass; ww, wet mass.
[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.

(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). However, experimental studies appeared to be highly influential in the effect estimates, because of extreme values and high leverage. Therefore, we carried out separate meta-analyses for correlative and experimental data sets.

(*a*) *Potential bias in effect size reporting*

To test for the presence of potential bias in the results of our meta-analysis, we first explored funnel plots produced between effect sizes and their corresponding measure of 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* function (*metafor* package, v. 2.4-0; Viechtbauer, 2010). Egger's test evaluates the relationship between effect sizes and measurements of study precision (Egger *et al.*, 1997), and can reveal different types of bias, such as reporting bias or poor methodological quality (Sterne *et al.*, 2011). For instance, studies reporting a significant effect may be more likely to be published than studies reporting no effect (Koricheva *et al.*, 2013; but see Koricheva, 2003). Here, most effect sizes for correlative studies, and all effect sizes for experimental studies, were extracted from published resources (Fig. 1). Our meta-analysis also included unpublished resources for the correlative data set. We thus tested (*i*) potential bias in published and unpublished studies separately, as well as combined; (*ii*) whether the publication status (used as a moderator) of the effect size had an effect on the meta-analytical results.

(*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 sources of non-independence. Our data were affected by multiple types of non-independence (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 well as non-independence of species (shared ancestry). We aimed to control for these dependencies by testing the effect of three random variables: individual effect size identity (individual effect size ID, unique per data row, necessary to estimate residual heterogeneity; Noble *et al.*, 2017), study identity (study ID), and species identity (species ID). In the 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 ultrametric consensus tree that was inferred from the *SumTrees* Python library (Sukumaran & Holder, 2010), based on 1000 random trees obtained from birdtree.org (Jetz *et al.*, 2012), using the Hackett backbone tree (Hackett *et al.*, 2008). Phylogeny was not accounted for in the experimental data set, as including phylogenetic random effects with less than 15 species can lead to unreliable estimates (Bolker *et al.*, 2009). To select the appropriate random structure, we constructed intercept-only meta-regression with all combinations of the three random variables, as well as the phylogenetic signal for correlative studies, using the maximum-likelihood (ML) method. We then compared the models using the Akaike Information Criterion (AIC) and chose the random structure of the model with the lowest AIC value, and lowest number of variables when AIC values were similar between models (parsimony criteria) (Table S3). Using the random structure of the best selected model, we tested the overall effect size of Hg contamination on body condition using restricted 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 *metafor*), without any random effects. I^2 represents the percentage heterogeneity in the effect sizes (0–100%) due to true heterogeneity rather than random sampling variance (Higgins & 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 life-history, ecological or physiological parameters could explain the high heterogeneity observed in the effect of Hg contamination on body condition in birds.

(*c*) *Moderator analysis*

In order to study the influence of different moderators on the association between Hg contamination and body condition, we constructed multifactorial meta-analytic models using the *MuMIn* package (Bartón, 2020). Chicks and adults, as well as blood and feathers, are known to behave differently in terms of Hg accumulation and health effects (e.g. Whitney & Cristol, 2018), and could show different associations between Hg and body condition. Therefore, their single and interactive effects were always accounted for in models of the correlative data set, as follows: z score ~ age class + tissue type + age class*tissue type + *Moderator* (Table S4). Models were constructed with the selected random structure (see Sections II.4*b* and III), fitted using ML, and compared to the base model: z score ~ age class + 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 available data on body condition and Hg concentrations in blood or feathers of juveniles were pooled with those of adults. We considered that a moderator had a significant effect on the association between Hg and body condition when its addition to the base model decreased the AIC corrected for small sample size (AICc) by at least 2. Data on BMR were available only for a subset of observations. To test the effect of BMR on the association between Hg and body condition we thus constructed a separate set of models (Table S4). Using these models, 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

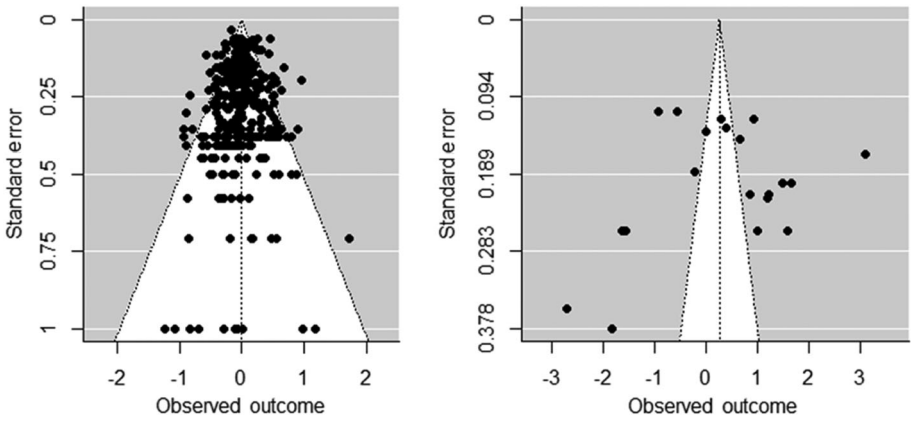

Fig. 2. Funnel plot for correlative (left) and experimental (right) studies.

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).

III RESULTS

(1) Bias in effect size reporting

For the correlative data set, Egger's tests indicated a tendency for biased reporting towards negative effect sizes among published studies (Egger's test: $N = 224$, $z = -1.932$, $P = 0.053$), and a significant bias towards positive effect sizes among unpublished studies (Egger's test $N = 91$, $z = 2.148$, $P = 0.032$; see Table S6 for funnel plots). By contrast, we found no statistical evidence of bias in the correlative database combining published and unpublished effect sizes (Egger's test: $N = 315$, $z = -0.707$, $P = 0.480$). In addition, publication status had no effect on the Hg–body condition association (Table S6). Therefore, all further meta-analytic models were only run on the full correlative data set combining published and unpublished effect sizes.

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

(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 wild populations, including mainly adult passerines and seabirds, from terrestrial and marine 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 multilevel meta-analytic models indicated a significant increase in fit with the inclusion of individual effect size ID and species ID (Table S3), which were retained in the random structure of all subsequent models. Phylogenetic signal appeared to have little influence on the overall effect size and did not affect model fit. The overall effect of Hg contamination on body condition was non-significant (estimate ± SE = −0.011 ± 0.020, confidence interval, CI [−0.049; 0.027], while accounting for individual effect size ID and species ID). Effect size heterogeneity was moderate ($I^2 = 55\%$; Cochran's Q test = 668, df = 314, $P < 0.0001$), indicating suitability for moderator analyses. Multifactorial moderator analyses revealed that wintering status had an influence on effect size estimates (AICc 2.6 points lower than the base model, Table S4): wintering birds were more likely to show a negative effect of Hg on body condition (Fig. 3). Other moderators had no clear effects on the Hg–body condition association (Table S4).

(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 moderator predicted the Hg–body condition relationship (Table S5, Fig. 4, $P > 0.100$ in all Omnibus tests).

IV DISCUSSION

Our extensive meta-analysis showed no overall effect of Hg contamination on body condition across 147 free-

Explanatory	Sample size	Level	95% confidence interval	p–value
Age class * Tissue + bird type	315	Passerine	[-0.082–0.033]	0.406
		Raptor	[-0.284–0.252]	0.907
		Seabird	[-0.035–0.103]	0.334
		Wader	[-0.307–0.019]	0.084
Age 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
Age class * Tissue + zone	315	Polar/subpolar	[-0.024–0.130]	0.175
		Temperate	[-0.088–0.024]	0.266
		Tropical/subtropical	[-0.119–0.060]	0.519
Age 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
Age class * Tissue + other var. acc.	315	No	[-0.054–0.042]	0.805
		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
Age 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
		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
		Yes	[-0.406– -0.025]	0.027
Age class * Tissue + log([Hg] ppm dw)	315	log([Hg] ppm dw)	[-0.028–0.035]	0.809
Age class * Tissue + log(BMR kJ/day)	132	log(BMR kJ/day)	[-0.044–0.024]	0.560

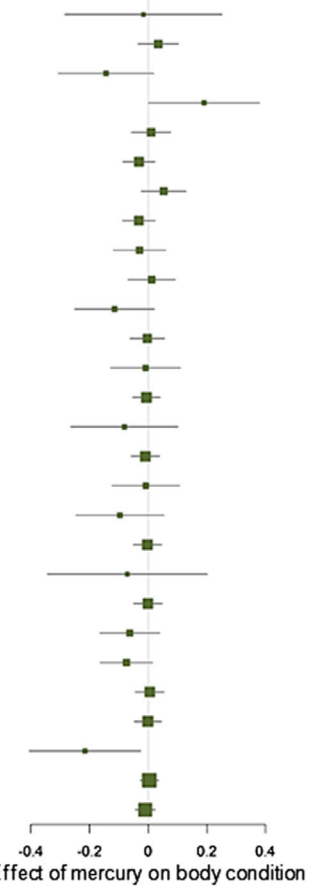

Fig. 3. Forest plot of the effect size for observed relationships between Hg concentrations and body condition in birds in correlative studies, depending on ecological, physiological and methodological factors (Fisher's $\tilde{z}$ scores [± 95% confidence interval]), while accounting for tissue type,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

living or captive bird species. However, free-ranging wintering passerines were more likely to present a negative association between Hg concentration and 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 especially migrating and overwintering birds, are underrepresented in the literature on Hg contamination and body condition. Experimental studies were more likely to detect a significant effect of Hg concentrations on body condition, with 90% of estimated effect sizes being significantly positive or negative. Conversely, only 14% of correlative effect sizes for the effect of Hg contamination on body condition were significantly positive or negative. Although recent experimental studies exposed birds to environmentally realistic Hg doses, 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 effects between correlative and experimental studies could stem from a threshold dose that can be reached under controlled conditions, but is unlikely in the wild.

(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

Explanatory	Sample size	Level	95% confidence interval	p–value
log([Hg] ppm dw)	20	log([Hg] ppm dw)	[-0.253–0.225]	0.905
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

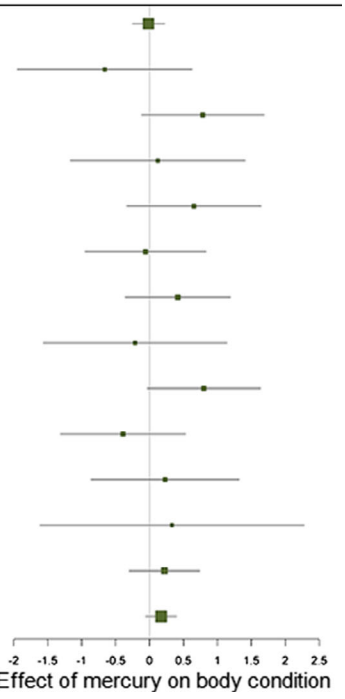

Fig. 4. Forest plot of the effect size for observed relationships between Hg contamination and body condition in birds in experimental studies, depending on ecological, physiological and methodological factors (Fisher's $\tilde{z}$ scores [± 95% confidence interval]). The dashed line represents a null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

references therein]. Experimental exposure to environmentally realistic Hg levels caused an increase in energy (fat) stores and body mass in zebra finch *Taeniopygia guttata* (Gerson *et al.*, 2019). Feeding 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 ducks *Anas platyrhynchos* exposed to Hg and fed *ad libitum* (Heinz, 1979). Alternatively, Hg could increase energy storage by disrupting the metabolism of carbohydrates or lipids [Seewagen (2020) and references therein]. However, in another experimental study, Hg-treated *Taeniopygia guttata* individuals waited longer to commence foraging and showed a significant decrease in their body mass, after exposure to predation risk (Kobiela *et al.*, 2015). Other experimental studies showed no effect of Hg on body condition despite reduced appetite, motivation to forage, and possibly low foraging efficiency (Bouton *et al.*, 1999; Spalding *et al.*, 2000; Adams & Frederick, 2008). Overall, experimental studies point to disruption of feeding behaviour, and/or nutrient and energy metabolism, with positive, negative or no consequences on body condition. This suggests that metabolic effects of Hg may be weak, and thus become (statistically) detectable only at high exposure levels, and/or under specific conditions that could not be identified by the meta-analysis. Experimental data 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 could reveal a different picture.

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

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 more likely to show a negative effect of Hg concentrations on body condition, suggesting a more detectable, negative effect when food is scarce and/or energetic demand for coping with unfavourable weather conditions is high. This effect was driven by two studies on several passerine species (Ackerman *et al.*, 2012, 2019) and needs confirmation from other species. As discussed above for metabolic and behavioural effects in experimental settings, food intake and predation risk could be critical in driving effects of Hg concentration on body condition. Feeding rates, food availability and predation risk are challenging to measure in the wild, and could thus be key factors potentially confounding the Hg–body condition association *in natura*. In conclusion, there is a need for further studies that measure Hg–body 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, overwintering and moult.

(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 al.* (2017) and Evers (2018), reproductive endpoints should be preferred to estimate Hg toxicity risk. Effects of Hg on reproductive success also have the advantage of being comparable between laboratory-based and field studies in similar taxa (Evers, 2018). The results of our meta-analysis also refute our prediction of smaller effect sizes of the Hg–body condition association in piscivorous species, because of their naturally high Hg exposure over 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 which are inherently linked to the concept of 'body condition'. Body condition indices have been used as indicators of fat reserves, although not always explicitly so (reviewed in Labocha & Hayes, 2012). However, body mass variation can be driven largely by lean mass, not only fat mass, especially in migrating birds (Piersma, Gudmundsson & Lilliendahl, 1999; Seewagen & Guglielmo, 2011). As such, body condition indices may be poor indicators of energy stores in species with intrinsically low percentage of body lipids (Jacobs *et al.*, 2012), and be no more informative than body mass alone (Labocha & Hayes, 2012). Here, we found no effect of body condition index type on the Hg–body condition association (Tables S2 and S4). Previous studies have shown that it is complicated to draw generalisations on which body condition index best represents body condition, but that different indices are often correlated (Labocha *et al.*, 2014; Kraft *et al.*, 2019). We can speculate that if Hg had a clear impact on 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 vary substantially with season, sex and other factors, complicating comparisons among studies (Labocha & Hayes, 2012; Labocha *et al.*, 2014). For instance, effects of Hg on body condition have been shown to depend on time of day in migrating passerines (Adams *et al.*, 2020b), as body mass can fluctuate strongly across the day in small birds. To investigate further the potential role of energy storage and use on the relationship between Hg concentration and body condition, we tested the effect of BM ratio and BMR as moderators. 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, post-absorptive phase, under thermoneutral conditions (McNab, 1997; Ellis & Gabrielsen, 2001; White *et al.*, 2007)]. Both species-specific BM ratio and BMR were poor predictors of the variation in the Hg–body condition association. However, only a third of the species included in the analysis had known BMR information, and BMR also can vary depending on 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 (Blévin *et al.*, 2017). The influence of energy storage strategies and BMR on the association between Hg contamination and body condition needs further investigation, and likely works at the individual level, which cannot be accounted for by meta-analytical approaches.

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 temporal integration of Hg into feathers and the timing of body condition measures (see also Section II.1). In addition, the Hg–body condition relationship could reflect mechanisms for dilution (or concentration) of Hg in tissues following body mass gain (or loss). However, this has been shown only in two studies on healthy individuals [Hg dilution in blood in growing 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 that died from starvation (Fort *et al.*, 2015). Further evidence from multiple avian species is necessary to confirm whether adaptive changes in body mass and body mass composition, which are necessary to sustain energy-demanding activities such as moulting, migrating and breeding (Bech, Langseth & Gabrielsen, 1999), could drive variation in circulating Hg 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.*, 2020b).

Another possible factor confounding the Hg–body condition association could be selenium (Se) status. Se can play a

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

V CONCLUSIONS

(1) Our meta-analysis indicates that body condition is an unreliable endpoint of the sublethal effects of Hg in wild birds.
(2) Associations of Hg with body condition appear to be clearer under controlled conditions and further investigations are needed.
(3) Wintering birds were more likely to show a negative association between Hg and body condition in the wild, but further studies should confirm this in additional taxa.
(4) We highlight a substantial knowledge gap on the metabolic effects of Hg in waders and raptors, birds in freshwater habitats and from tropical/subtropical regions, and especially in migrating and overwintering birds.
(5) Our results indicate the need for further studies in both the laboratory and the field on the effects of Hg on feeding rates, foraging efficiency, and energy storage and use in a larger sample of individuals and species.

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VIII. Supporting information

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

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