Environmental Science & Technology

Article

Cite This: *Environ. Sci. Technol.* 2019, 53, 7821−7829

pubs.acs.org/est

Effects of Maternal Reproductive Investment on Sex-Specific Pollutant Accumulation in Seabirds: A Meta-Analysis

Daniel J. Hitchcock,*[,†] Tom Andersen,[†] Øystein Varpe,[‡,§] and Katrine Borgå*[,†]

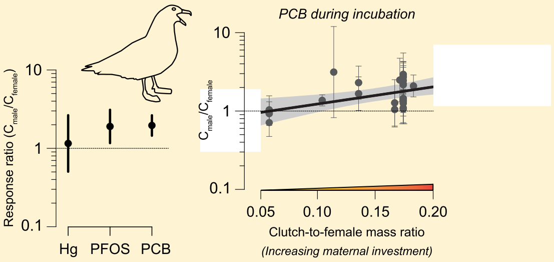
[†]Department of Biosciences, University of Oslo, 0316 Oslo, Norway

[‡]Department of Arctic Biology, University Centre in Svalbard, 9171 Longyearbyen, Norway

[§]Norwegian Institute for Nature Research, 5006 Bergen, Norway

Supporting Information

ABSTRACT: Avian egg production demands resources such as lipids and proteins. Relative egg size and mass varies across species, reflecting differences in maternal investment. This variability may affect the maternal transfer of anthropogenic pollutants including lipophilic polychlorinated biphenyls (PCBs) and protein-associated per- and polyfluoroalkyl substances (PFASs) and mercury (Hg). We conducted a meta-analysis on seabirds and investigated whether interspecies variation in maternal investment contributes toward skewed pollutant concentration ratios between males and females, as C_{male}/C_{female} (80 studies). Overall concentrations of PCBs and perfluorooctanesulfonic acid (PFOS) were 1.6 and 1.3 times higher, respectively, in males than females, whereas mercury was similar between sexes. Few studies compared females and eggs ($n = 6$), highlighting a knowledge gap. We found that an increasing maternal investment as a clutch-to-female mass ratio resulted in lower PCB concentrations in females than in males during the incubation period, but no sex-specific differences were observed for mercury and PFOS. Egg production is both a lipid dominated and protein-limited process. Females transfer lipophilic pollutants more easily to eggs, and to a higher degree with increasing maternal investment, but feeding ecology may be more important. Interspecies variation in maternal pollutant transfer may lead to negative effects scaling from an offspring to population level.



INTRODUCTION

Life history theory can help us predict how an individual acquires and allocates resources while maximizing fitness.[1] Resources, such as lipids and proteins, directed toward reproduction have been studied in great detail, particularly in the context of avian egg production. The large variability in clutch size across avian taxa can be explained by life history trade-offs between maternal investment and offspring survival.[1,2] In particular, the relative availability of different nutrients may affect clutch size, with proteins serving as limiting resource during egg production.[3,4]

Egg laying serves as one major route of pollutant excretion.[5,6] Egg production includes the transfer of nutrients from maternal reserves to developing ovarian follicles, in combination with anthropogenic pollutants.[7] Pollutants such as persistent organic pollutants (POPs) and mercury (Hg) are known for their bioaccumulative and toxic properties.[8,9] Such chemicals can exert negative effects scaling from an individual to population level.[10−12] POPs include organohalogentated compounds such as polychlorinated biphenyls (PCBs) and perfluorooctanesulfonic acid (PFOS).[8] PCBs, mercury, and PFOS accumulate in avian tissue and are soluble in different macronutrients: PCBs are lipophilic, whereas mercury and PFOS are protein-associated.[7,13,14]

Variation in pollutant concentrations across bird species is largely attributable to biological factors such as seasonal changes in body lipids, trophic position, and feeding ecology.[15,16] Pollutant transfer from mother to offspring (maternal transfer) may also lead to skewed concentration ratios between sexes during breeding, with males possessing a higher concentration of pollutants than females.[17] Reproductive status may also affect concentration ratios between sexes, where effects may disappear during the nonbreeding periods,[18] as females reach steady-state concentration.[19] The effects of reproductive strategy on pollutant bioaccumulation have been explored within avian species including ring doves (*Streptopelia risoria*) and herring gulls (*Larus argentatus*).[20,21] Interspecies comparisons have been explored in marine mammals,[22] and also in birds but only on a single pollutant basis.[18] If the resources directed toward egg production are related to maternal pollutant elimination, then an increasing maternal investment should also result in lower pollutant concentrations in reproducing females than in males. Given that protein serves as a limiting resource during egg production,[4] then maternal investment may have a greater effect on the transfer of lipophilic PCBs than protein-associated mercury and PFOS.

Received: March 1, 2019
Revised: May 23, 2019
Accepted: May 28, 2019
Published: May 28, 2019

ACS Publications

DOI: 10.1021/acs.est.9b01296

To synthesize individual studies reporting pollutant concentrations in eggs and adult seabird species, we conducted a meta-analysis. We choose seabirds as our target group when exploring the effect of life history variation while minimizing the confounding effects of phylogeny, trophic position, and dietary specialization across habitats. We quantify maternal investment as the proportion of a female's body mass relative to her clutch of eggs, and sexual dimorphism as the body mass ratio between males and females. Lipophilic PCBs, and protein-associated mercury and PFOS represent our model compounds, as we have a strong understanding of their physicochemical properties, including their association to different macronutrients involved in egg production. We also expect data to be most sufficient for these chemicals to allow for robust analysis.

We test the effect of maternal investment as a mechanism of pollutant excretion in females. We test four hypotheses: (1) species that invest more resources toward clutch production will transfer more pollutants from mother to egg; (2) species that invest more resources toward a clutch will result in lower concentrations in females than males; (3) effects of maternal investment on pollutant concentration differences will be greatest during the incubation period; and (4) maternal investment has a greater effect on transfer lipophilic pollutants (PCB) than that of protein-associated pollutants (mercury and PFOS).

■ MATERIALS AND METHODS

Literature Search and Data Extraction. We searched for all peer reviewed, published studies reporting pollutant concentrations in seabirds on the Web of Science (v. 5.27.2) Core Collection database for all years up to 15-Feb-2018. Our literature search included search terms for pollutants as well as a combination of common and Latin names for all seabird species (see Supporting Information, SI, for keywords used). We first filtered articles according to title, year, and abstract, while keeping all other details blind. During the title-abstract screening, we considered all types of anthropogenic organic pollutants except radionuclides, natural toxins, and trace elements other than mercury. We considered all seabird tissues and pollutant data collected from all observational studies. If it was unclear whether a study was relevant, then we included it for further assessment. We then screened full-text articles for eligibility if they:

(1) Measured halogenated anthropogenic pollutants or mercury in one or more seabird species as part of an observational field study;
(2) Reported separate measurements for either: (i) male and female; or (ii) egg and female, with adults at sexual maturity;
(3) Measured pollutants in internal tissues and/or organs;
(4) Reported mean pollutant concentrations, standard deviations (SD), and sampled sizes (*n*), or allowed them to be calculated.[23]

Studies measuring pollutants in individuals from laboratory or zoological garden studies were not considered for full-text assessment. Studies measuring carcasses were only included if mortality was recent, i.e., within days of sampling. We included studies reporting pollutant levels in liver, kidney, muscle, and fat tissue, as these represented the most measured tissue matrices across studies. We only considered studies with adults that had reached sexual maturity, and excluded studies with data from individuals with unknown or mixed age groups (e.g., combination of chick, juveniles, and/or adults). If repeated sampling of individuals took place, then we only used data from the first sampling effort.

After full-text screening, we included three pollutants for meta-analysis: PCB, mercury, and PFOS. We treated these data separately since these chemicals have different binding affinities to lipids and proteins. We required PCB concentration on lipid weight basis, because lipid content may vary across tissue matrix and species.[15] We used reported lipid adjusted concentrations or calculated these from reported wet weight concentrations and lipid content. When possible, we obtained the concentrations of the dominating congener PCB-153, but otherwise assumed PCB-153 to be the dominant congener when a sum of PCB concentrations was reported.[24] For mercury, we required concentrations to be expressed on dry weight basis, and assumed 80% moisture content in liver, muscle, and blood for conversion if dry mass was not known or provided.[25] For PFOS, we required all studies to report concentration on a wet weight basis, and included concentrations from the linear isomer of the chemical when possible. For male−female comparisons, we required pollutant concentrations to be reported in the same tissue matrix for both sexes. For egg-female comparisons, we required pollutant concentrations to be reported on a whole egg basis. We also recorded information on tissue matrix and breeding status (prebreeding, incubation, postbreeding, nonbreeding, mixed, or not specified).

We extracted mean pollutant concentrations, SDs and sample sizes from individual studies from the main text, tables, and figures, SI, or calculated these values from individual measurements. We used the selection tool in ImageJ (v. 1.51k) to estimate concentrations and variability when data were presented in figure format.[26] Our final data sets for PCBs, mercury, and PFOS include one which compares pollutant concentrations in egg-females, and one which compares male to females.

Effect Size Calculations. We calculated the log response ratio (LRR) as our effect size since pollutant concentrations represent a continuous positive variable and often take a log-normal distribution. LRR is represented as the mean pollutant concentration in one group of individuals divided by another such that,

$$\mathrm{LRR} = \ln \frac{C_{\mathrm{male}}}{C_{\mathrm{female}}} \tag{1}$$

where *C* refers to the concentration of a given pollutant (PCB as lipid weight, mercury as dry weight and PFOS as wet weight). An LRR greater than 0 means that the concentration of a given pollutant is greater in males than in females, and vice versa. Variance is calculated as follows:

$$\mathrm{var(LRR)} = \frac{(\mathrm{SD}_{\mathrm{male}})^2}{N_{\mathrm{male}}(C_{\mathrm{male}})^2} + \frac{(\mathrm{SD}_{\mathrm{female}})^2}{N_{\mathrm{female}}(C_{\mathrm{female}})^2} \tag{2}$$

where SD and *N* represent the standard deviation and sample size of each group from each study.[27] LRR and var(LRR) values are used for statistical analyses. However, for ease of interpretation in the remainder of this text, we express effect size as the exponent of LRR, the response ratio (RR). Here, a RR of 1 represents equal pollutant concentrations between sexes.

DOI: 10.1021/acs.est.9b01296
Environ. Sci. Technol. 2019, 53, 7821−7829

Quantifying Maternal Investment and Sexual Dimorphism. We extracted life history measures from seabird databases including adult body mass (male and female when possible), clutch size, and egg mass. Most studies reporting pollutant data either did not measure or provide life history estimates, prompting us to use population averages from databases. Additionally, we were interested in the interspecies variation in life history traits rather than differences within species. When possible, we extracted life history trait information using the CRC Handbook of Avian Body Masses, AnAge database, and Handbook of the Birds of the World.[28−30] When life history information was missing from databases, we extracted estimates from individual studies (Table S3, SI).

One approach to quantify maternal investment involves calculating the ratio between the mass of a clutch with the mass of an adult female (as $[n_{\text{egg}} \times m_{\text{egg}}]/m_{\text{female}}$). Assuming that producing a clutch is energetically costly,[31,32] an increasing maternal investment implies greater relative amount of energy or resources directed toward egg production. For example, an Adelie penguin *Pygoscelis adeliae* clutch constitutes less than 10% of an adult female's body mass, whereas a mallard *Anas platyrhynchos* clutch can represent 40% the mass of an adult female.[33] Assuming all other routes of pollutant elimination are similar between sexes, interspecies variation in maternal clutch investment should reflect the degree to which females transfer pollutants to their eggs and thus lead to skewed concentration ratios between sexes, assuming that exposure routes are also comparable.

Many seabird species exhibit sexual dimorphism in body size. Larger-bodied individuals may have higher energetic demands than smaller individuals,[34] meaning that pollutant concentrations could increase with body size but these effects are likely limited.[18] We explored the potential effect of sexual dimorphism on pollutant concentration ratios between sexes by calculating the adult mass ratio between males and females (as $m_{\text{male}}/m_{\text{female}}$). For species where only a single body mass estimate was available, we assumed sexes were similar and set the male-to-female mass ratio to one (Table S3, SI).

Statistical Analyses. We tested whether pollutant concentration ratios varied between sexes by meta-analysis. We also tested whether differences in tissue matrix, breeding status, maternal investment, and sexual dimorphism contributed toward differences in pollutant concentration ratios across species.

For each pollutant, we calculated a grand mean of RR and 95% confidence interval using the RR, variances and weighting factors derived from each study.[35] Weighting factors ($w_i = 1/\text{var}_i$) gives studies with high precision (smaller variance and higher sample size) greater weighting than studies with low precision (larger variance and smaller sample size). An effect size with a confidence interval that does not overlap a RR of 1 implies a significant difference between males and females.[27] For each pollutant, we also calculated the Q-score and I^2 index—heterogeneity statistics that represent the proportion of unexplained between-study variation. An I^2 greater than 50% suggests that between-study variation is substantial and can be further explored by meta-regression analysis.[36] We also calculated Hedges' g, commonly used in meta-analysis, as an effect size which yielded the same results (Table S4, SI).

We considered the effect of tissue matrix and breeding status as confounding factors, and tested their effect using subgroup analysis. Nonoverlapping effect sizes may imply significant differences between categorical variables. We then analyzed the relationship between concentration ratio between sexes and (1) maternal investment in clutches (expressed as clutch-to-female mass ratio); and (2) sexual dimorphism (expressed as male-to-female mass ratio) by meta-regression. Models were developed using a mixed-effects meta-analytical model.[37] We included study and species as categorical random factors, since studies vary in sampling period and location; and closely related species may respond more similarly than distantly related ones.[38] When considering species as a random factor we constructed a phylogenetic correlation matrix using consensus tree based on subset tree from available phylogenetic data,[39] and included this matrix as an additional random factor in our mixed-effect model (SI). Models were fitted using a restricted maximum likelihood (REML) approach, which is best suited for models with mixed or multilevel effects.[35]

Maternal investment and sexual dimorphism were included as explanatory variables in separate mixed-effect models, and were compared to null models containing no fixed or random effects. The explanatory power of included variables was calculated using a pseudo-R^2 value, which represents the proportional reduction in total variance of a full model compared to its null model (as $[\sum\sigma^2_{\text{null}} - \sum\sigma^2_{\text{model}}]/\sum\sigma^2_{\text{null}}$, where σ^2 is an estimator for between-study variance). We carried out all analyses in R (v. 3.4.1), using the APE and Metafor packages for phylogenetic and meta-analyses, respectively.[40−42] We set the significance level α to 0.05 in all our models, and present estimates and models as means and 95% confidence intervals unless specified otherwise.

RESULTS AND DISCUSSION

Summary of Data Sets. A literature search of 2941 seabird studies returned six studies on egg-females and 37 studies on male−females. The egg-female data set reported pollutant concentrations in six species, however we could not conduct formal meta-analysis due to the limited number of studies available (Tables 1 and 2). In the male−female data set, pollutant concentrations were reported in 27 species, with mercury concentrations reported at the highest frequency followed by PCB and PFOS (mercury = 42%; PCB = 39%; PFOS = 19%; Table 1).

Concentration Sex Ratios. PCB and PFOS concentrations were 1.64 and 1.28 times higher in males than in females, respectively (PCB: CI_{95} = 1.14−2.36; range: 0.71−6.48; $P = 0.007$; PFOS: CI_{95} = 1.00−1.64; range: 0.30−2.40; $P = 0.054$). Mercury concentrations were similar between sexes (RR = 1.08; CI_{95} = 0.55−2.12; range: 0.44−2.58; $P = 0.82$;

Table 1. Number of Studies That Allow Comparison of Pollutant Concentrations between Eggs and Females, as Well as between Females and Males[a]

	number of comparisons from N studies	
	egg-female	male−female incubation data/all data
PCB	2 from 2 studies	24/31 from 19 studies
mercury	2 from 2 studies	14/33 from 17 studies
PFOS	3 from 2 studies	6/15 from 9 studies
total	7 from 6 studies	44/79 from 37 studies

[a] For male-female studies, the number of comparisons during the incubation period is also indicated. Some studies report pollutant concentrations for multiple species.

Table 2. Response Ratio and Variance of Pollutants Measured Egg-Females of Various Seabird Species, As Well As Pollutant Group, Tissue Matrix, Concentrations and Sample Sizes[a]

study	species	pollutant group	female tissue matrix	C_{egg}	N_{egg}	C_{female}	N_{female}	response ratio (C_{egg}:C_{female})
Verreault 2005	Glaucous gull (*Larus hyperboreus*)	PCB[b]	plasma	11786 ± 3604	30	31646 ± 16863	42	0.37
Verreault 2006	Glaucous gull (*Larus hyperboreus*)	PCB	plasma	11130 ± 13820	10	11130 ± 13820	10	0.38
Lewis 1993	European Herring gull (*Larus argentatus*)	mercury[c]	liver	1430 ± 640	26	4370 ± 1760	27	0.33
Robinson 2011	Double-crested cormorant (*Phalacrocorax auritus*)	mercury	liver	1100 ± 100	8	4400 ± 2165	18	0.25
Bertolero 2015	Yellow-legged gull (*Larus michaehellis*)	PFOS[d]	blood	75 ± 31	34	27 ± 17	17	2.75
Bertolero 2015	Audouin's gull (*Larus audouinii*)	PFOS	blood	88 ± 23	36	25 ± 12	12	3.49
Herzke 2009	European shag (*Phalacrocorax artisotelis*)	PFOS	liver	37 ± 21	6	29 ± 11	6	1.29

[a] Concentrations are reported as mean ± standard deviation. [b] Polychlorinated biphenyl (PCB) concentrations reported as ng g^{-1} lipid weight. [c] Mercury (Hg) concentrations reported as ng g^{-1} dry weight. [d] Perfluorooctanesulfonic acid (PFOS) concentrations reported as ng g^{-1} wet weight. [e] C_{egg} = average concentration of pollutants in eggs; C_{female} = average concentration of pollutants in eggs; n = sample size of each group.

Figure 1). The proportion of unexplained between-study variation was large for all pollutant groups (PCB: $Q_E = 111.6$; $I^2 = 82.5\%$; $P < 0.001$; mercury: $Q_E = 198.3$; $I^2 = 96.3\%$; $P < 0.001$; PFOS: $Q_E = 50.0$; $I^2 = 95.1\%$; $P < 0.001$). For PCBs, breeding status was important (24 out of 31 studies) when considering differences in concentration sex ratios ($Q_M = 11.0$; $R^2 = 15.1\%$; $P = 0.026$), with differences between males and females being largest when comparing individuals during the incubation period. For mercury and PFOS, breeding status did not contribute to differences pollutant concentrations, and tissue matrix did not contribute to differences in concentrations for all pollutant groups (Table S7, SI).

During incubation, female seabirds contained lower levels of PCBs than males, supporting our expectation that egg production serves as a major route of excretion for lipophilic pollutants, given that exposure to PCBs was similar. Lipids constitute approximately 20−30% of total egg mass,[43] with both lipids and PCBs being almost exclusive to egg yolk.[44] The remainder of the egg contains protein, carbohydrate, and water, which are divided between albumen and yolk.[45,46] Mercury is predominantly found in the albumen compartment of eggs,[47,48] which females can form in as little as 1 day.[46,49] Some species acquire resources for albumen production exclusively from local diet as opposed to body reserves.[50] However, egg lipids can take several weeks to form and likely derive from body reserves (capital breeding) than recently acquired dietary resources (income breeding).[33,43] Egg formation may be a protein-limited process, with increased protein in diet increasing clutch size in some birds.[4,31] These findings suggest that either females transfer lipophilic pollutants more easily than protein-associated pollutants during egg production, or that egg production is a lipid dominated process. However, PFOS is both protein-associated as well as lipophilic, binding to both serum albumin and lipoproteins, respectively.[51−53] In biological tissues, PFOS concentrations increase with increasing lipid content,[54] meaning that PFOS is likely affected by similar biological processes as PCB. However, the additional protein-associated properties of PFOS may result in weaker sex specific differences as reflected by the findings in the present study.

PCB concentrations were higher in males than in females during the incubation period. One explanation could be that the partitioning of PCBs from female body stores to egg yolk does not reach equilibrium by the time egg formation is complete. Lipid-normalized organochlorine concentrations in female muscle tissue are higher than in eggs across several bird species,[5] suggesting PCB deposition in eggs is a rate-limited process.[55] However, the limited number of studies available comparing pollutant concentrations between eggs and females as well as egg-mother pairs indicates a knowledge gap. The two studies that reported PCB concentrations in eggs and females also indicate a skewed concentration ratio, with eggs containing a lower concentration of PCBs than females.[44,56] Birds are capable of de novo synthesis of lipids from carbohydrates stored in liver tissue.[20] Given that eggs contain a large proportion of lipids,[43] then lipid synthesis during egg production may result in increased lipid content in females and consequently an apparent increased dilution of PCBs. Lipid content in serum was similar between sexes across all species included in our data set, suggesting that lipid dynamics during egg production does not affect circulating lipids in blood. In addition, we did not detect any differences in concentration ratios of PCBs between sexes when accounting for tissue matrix.

Sex-specific differences in PCB concentrations disappeared when we included studies containing individuals sampled outside of the incubation period. These additional studies reported pollutant concentrations in individuals with mixed and unknown breeding statuses as well as in nonbreeding individuals. Therefore, sex-specific differences may be the largest during the incubation period, shortly after females have produced a clutch. Additionally, females may utilize lipids to maintain body condition and energetic costs associated with egg incubation,[57] which may also lead to remobilised concentrations of PCBs. In the northern fulmar *Fulmaris glacialis*, females contained a lower concentration of PCBs than males during incubation, however concentrations were similar between nonbreeding females and males.[17] Pollutant concentrations between females and males may quickly reach equilibrium after producing a clutch,[18] which may explain the interaction between breeding status and concentration sex ratios in our data set.

A previous meta-analysis found overall lower concentrations of mercury in females than in males across a wide range of avian taxa, as well as for those sampled during the prebreeding and incubation periods.[18] In our study, however, we did not detect sex specific differences in mercury concentrations even when considering the effect of breeding status, regardless of

DOI: 10.1021/acs.est.9b01296
Environ. Sci. Technol. 2019, 53, 7821−7829

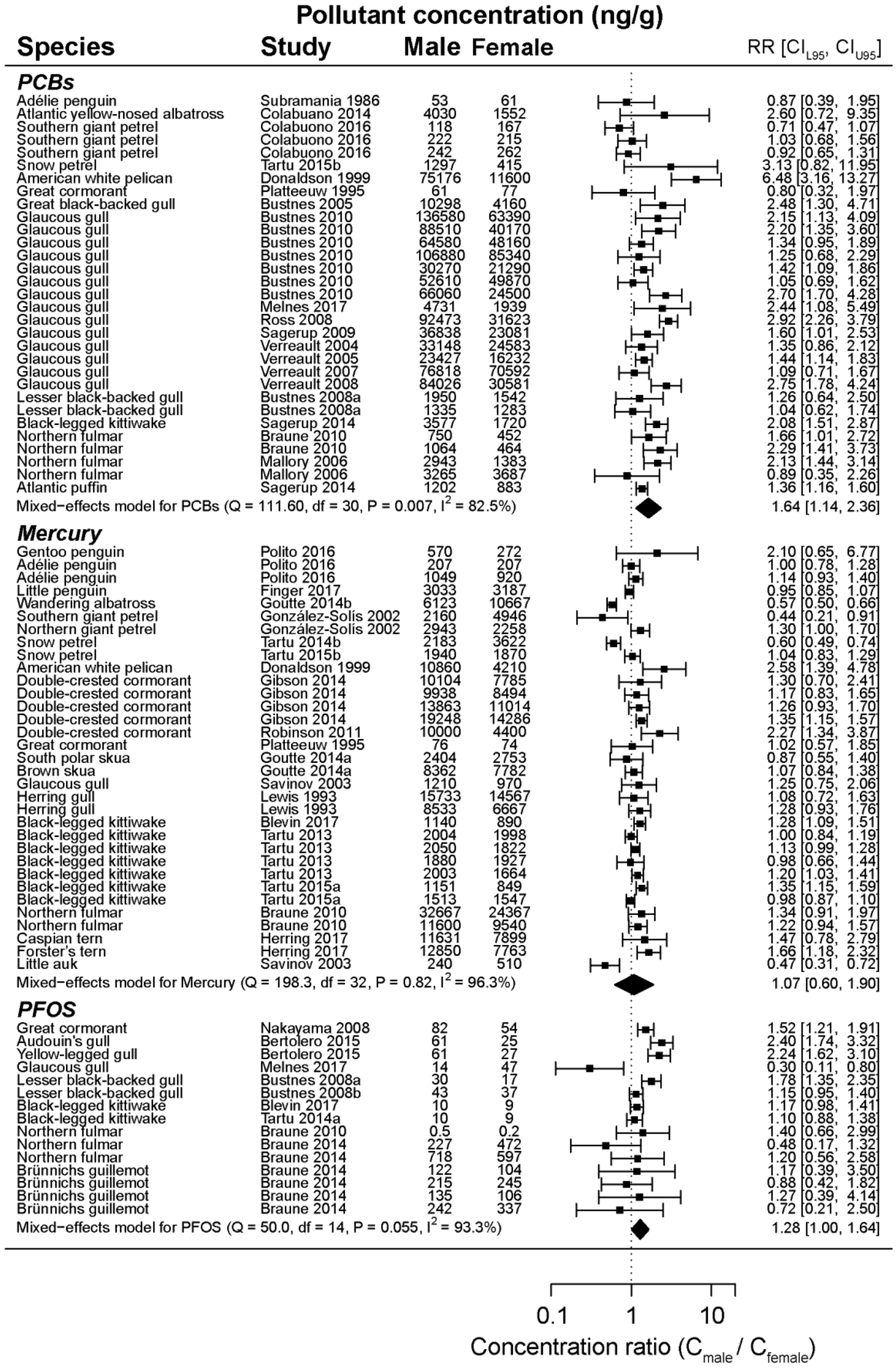


Figure 1. Concentration ratios (C_{male}/C_{female}) of PCBs, mercury, and PFOS between male and female seabird species, including overall effect sizes. Tissues include abdominal fat, liver, muscle, red blood cells, whole blood, and plasma. Concentrations for PCBs are on lipid weight basis; dry weight basis for mercury; and wet weight basis for PFOS. A full list of the relevant studies are included in the SI.

Table 3. Summary Statistics of Meta-Regression Models Tested in This Study, Between Various Explanatory Variables and Pollutant Concentration Ratios (C_{male}/C_{female}) of Different Pollutants, Including PCB, Mercury, and PFOS

explanatory variable	breeding considered?	*N*	intercept ± SE	slope ± SE	R^2 (%)	*P*-value
PCB						
clutch-to-female mass ratio	no	31	1.15 ± 1.35	16.00 ± 7.71	13.8	0.175
clutch-to-female mass ratio	yes	24	0.75 ± 1.33	167.63 ± 5.76	53.2	0.003
male-to-female mass ratio	no	33	8.56 ± 4.36	0.24 ± 3.44	0	0.145
mercury						
clutch-to-female mass ratio	no	33	1.21 ± 1.47	0.37 ± 5.98	0	0.580
male-to-female mass ratio	no	33	0.68 ± 2.39	1.52 ± 2.13	0	0.558
PFOS						
clutch-to-female mass ratio	no	15	0.87 ± 1.49	10.94 ± 9.83	15.1	0.295
male-to-female mass ratio	no	15	2.15 ± 2.43	0.63 ± 2.17	0	0.550

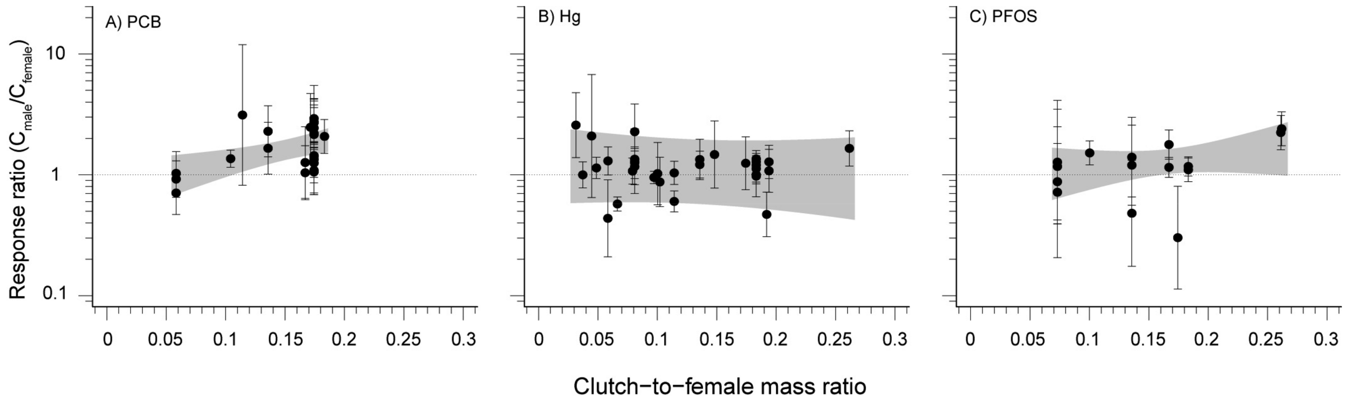


Figure 2. Relationship between maternal investment and the pollutant concentration ratio (C_{male}/C_{female}) of (a) polychlorinated biphenyl (PCB); (b) mercury (Hg); and (c) perfluorooctane sulfonic (PFOS) in seabirds. Shaded area represents the predicted mixed-effects meta-regression model. For PCBs, only species sampled during incubation have been included.

choice in effect size (RR or Hedges' g). A major difference between the two studies is that we only considered concentrations in seabird species, as we were interested in exploring the effect of life history variation across species with similar biology. This meant that we excluded mercury data from terrestrial bird species, freshwater birds, and sea ducks. We also included a broader range of tissue matrices, including muscle, and whole blood and red blood cells as concentrations were most frequently measured in these matrices. Our meta-analysis included additional publications comparing male−female seabirds after the 2012 study,[18] thus increasing our sample size and statistical power. These differences in inclusion criteria may have led to a difference in the overall effect size. Updated meta-analyses can sometimes conflict with previous findings.[58,59] However, the statistical methods carried out in this study are similar to the former study, suggesting instead that the robustness of the data has increased.

Effect of Maternal Investment. The clutch-to-female mass ratio ranged from 3% in the American pelican *Pelecanus erythrorhynchos* to 26% in several Larid genera (*Larus* and *Sterna*), with a median mass ratio of 10%.

For PCBs, we found that an increasing maternal investment toward a clutch resulted in higher concentrations in males than in females during incubation ($R^2 = 53.2\%$; $P = 0.003$; Table 3 and Figure 2a). This effect disappeared when combining seabirds of all breeding statuses ($R^2 = 13.8\%$; $P = 0.18$; Table 3). PCB concentrations during the incubation period were dominated by studies on the glaucous gulls *Larus hyperboreus* (13 out of 24 studies), which has a clutch-to-female mass ratio of 17%. We analyzed the sensitivity of the meta-regression analysis by removing this species, and still found a positive relationship between maternal investment and male−female RRs ($R^2 = 76.0\%$; $P = 0.004$). This suggests there is a robust relationship between maternal investment and pollutant concentration ratios between sexes. For mercury and PFOS, we found no relationship between maternal investment and male−female RRs (mercury: $R^2 = 0\%$; $P = 0.44$; PFOS: $R^2 = 15.1\%$; $P = 0.30$; Table 3 and Figure 2b and c), even when only comparing seabirds sampled during the incubation period.

During incubation, females with large clutches relative to their body mass may transfer a greater proportion of lipophilic pollutants to their eggs than females that produce smaller clutches. Sphenisciformes (penguins) and Procellariiformes such as petrels and albatrosses represent species with a low clutch-to-female mass ratio, i.e., lay one or two eggs per clutch, and PCB concentrations were similar between sexes. However, Charadriiformes such as gulls, terns, and auks represented species with the highest clutch-to-female mass ratios, and during the incubation period, those females contained lower concentrations of PCBs than males. We assumed that the allocation of resources toward egg production is closely related to the proportion between a female's body mass and clutch mass. However, the clutch-to-female ratio may only account for a small proportion of variation in maternal pollutant transfer. Additional factors such as female quality and food availability may better represent the potential effects of maternal investment on pollutant transfer,[60] as these variables more realistically describe a female's capacity to allocate resources toward egg production.

The lack of relationship between maternal investment and protein-associated pollutants may imply that maternal transfer has a weaker effect on protein-associated mercury and PFOS than lipophilic pollutants such as PCBs during the incubation period. Alternatively, mercury and PFOS deposited in the albumen may reflect exposure from a female's local diet during egg production,[61,62] which may limit her capacity to eliminate mercury and PFOS from stored body reserves. It is also possible that the dissolving capacity of mercury and PFOS in proteins is less than for PCBs in lipids. Reproductive strategies that influence different macronutrients and egg compartments warrant further investigation,[63,64] especially when pollutants exhibit different binding affinities to each type of macronutrient.

■ ADDITIONAL SEX-SPECIFIC EFFECTS

When body mass estimates were reported for both sexes as a proxy for sexual dimorphism, male−female mass ratios ranged between 1.06 and 1.32, with males always weighing more than females. Sexual dimorphism was unrelated to concentration sex ratios of all pollutants types (PCB: R^2 = 0%; P = 0.89; mercury: R^2 = 0%; P = 0.97; PFOS: R^2 = 0%; P = 0.53; Table 3). The lack of effect remained even when accounting for breeding status (Table S8, SI).

Differences in pollutant concentrations between sexes could also be explained by sex-specific differences in feeding ecology, which may mask the apparent effects of maternal investment and body size differences. For example, larger-bodied individuals may have the capacity to prey on larger food items than smaller-bodied individuals. Diet items such as fish may increase in age with increasing size class, and have a reduced capacity to eliminate pollutants.[15] Therefore, dietary differences due to sexual dimorphism may result in varying exposure to pollutants. Some seabird species such as skuas (*Stercorarius* spp.) have reverse sexual dimorphism, i.e. females are larger than males, but incubating females still contained lower concentrations of pollutants than males.[65,66] In some species, feeding behavior varies between sexes, e.g., Gentoo penguin *Pygoscelis papua* males feed on a higher trophic level than females,[67] resulting in higher exposure to biomagnifying pollutants.[15] Similarly, subantarctic breeding wandering albatrosses *Diomedea exulans* have gender specific feeding ecologies, which may explain differences in mercury and organic pollutant concentrations.[68] Feeding ecology information is often lacking for many seabird species, meaning that we could not account for differences in pollutant concentrations due to sex specific feeding behaviors.

Other components of life history variation may also play an important role when assessing concentration ratios between sexes. Factors such as the lifespan of an individual and age at first reproduction could impact overall pollutant concentration ratios across species. For example, the wandering albatrosses commence breeding from ten years of age,[69] while glaucous gulls can begin at five years of age. Birds that migrate to breed may utilize resources of varying pollutant profiles,[70] which when combined with sex-specific differences in feeding ecology, may have consequences on overall pollutant concentration ratios. Testing the effect of these life history traits was beyond the scope of this study, but improved and more transparent data reporting may allow for these factors to be tested in future meta-analyses.[23] While we only considered the effect of maternal investment in seabirds, the inclusion of other avian species or consideration of feeding ecology and physiology in future studies may further resolve differences in sex-specific pollutant concentrations across avian taxa.

Resources directed toward reproduction can have implications on how lipophilic pollutants such as PCBs are transferred from mother to offspring. Embryos and chicks represent a sensitive life stage of pollutant exposure,[71−73] and our analyses suggest that seabird species that allocate more resources into their clutches and may transfer more pollutants. However, the exposure of embryos to pollutants may also depend on additional biological factors such as clutch size and laying sequence.[44] Seabirds are long-lived organisms, and species with a late age at first reproduction (e.g., Procellariiformes) may also place their first clutches at greater risk, given that pollutants accumulate for a longer period before females of these species lay their first clutch. Although untested, this may have consequences on chick growth, development, and survival,[74,75] and further ecological effects, such as pollutant exposure in predators that specialize on bird eggs. Our findings that males contain higher concentrations of PCBs and PFOS than females could contribute to sex-specific effects, which may include reduced breeding probability or survival rates.[19,76] Taking into account variability in reproductive strategies across organisms is also important when modeling the predicted effects of pollutants scaling from individuals to populations,[10,77] given variability in life history across organisms. While many studies in ecotoxicology are species-specific, meta-analysis serves to bridge species information by synthesizing study data across many species. This in turn improves our general understanding of the biological processes that contribute to pollutant bioaccumulation, including the complex processes of resource allocation and reproductive effort, and their links to life history variability.

■ ASSOCIATED CONTENT

Ⓢ Supporting Information

The Supporting Information is available free of charge on the ACS Publications website at DOI: 10.1021/acs.est.9b01296.

> Search strategy flowchart (Figure S1); list of PCB congeners used when comparing studies (Tables S2−S3); life history estimates (Table S4); phylogenetic trees of the included seabird species (Figures S2−S3); summary statistics of meta-analyses (Tables S4−S8); meta-regression between maternal investment and PCB concentration sex ratios without accounting for breeding status (Figure S4); and meta-regression between sexual dimorphism and pollutant concentration sex ratios (Figure S5) (PDF)

■ AUTHOR INFORMATION

Corresponding Authors

*E-mail: daniel.hitchcock@ibv.uio.no.
*E-mail: katrine.borga@ibv.uio.no.

ORCID

Daniel J. Hitchcock: 0000-0001-7683-6128
Katrine Borgå: 0000-0002-8103-3263

Notes

The authors declare no competing financial interest.
The data set[78] used in this study is available at Figshare: https://doi.org/10.6084/m9.figshare.8188226

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