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Gulls foraging in highly urbanized areas experience disruption in hormones and energetic metabolism

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ABSTRACT

Studies on birds breeding in highly urbanized environments have reported high plasma levels of a range of halogenated flame retardants (HFRs) and per- and polyfluoroalkyl substances (PFAS). Exposure of birds to these organohalogens may disrupt hormone regulation and energy metabolism, potentially leading to adverse effects on reproduction and health. While the sources and pathways of exposure to certain of these organohalogens have been documented in several bird populations, little information is available on the exposure-related effects on hormones involved in energy metabolism and their cascading effects on metabolism and energy expenditure. This study aimed to assess the linkages between plasma concentrations of PFAS and HFRs, and thyroid hormones, glucocorticoids, as well as other markers of energy metabolism in nesting ring-billed gulls (*Larus delawarensis)* for which foraging movements were tracked for three years in the Montreal area (QC, Canada). Plasma HFR and PFAS concentrations did not vary with foraging habitat use patterns, suggesting diffuse urban sources. Plasma HFR and PFAS concentrations were associated with sex-specific hormonal and metabolic responses. Specifically, lipid-derived β-hydroxybutyrate levels in plasma of males significantly decreased with increasing PFAS concentrations, whereas this relationship was positive in females. Furthermore, triiodothyronine (T_3) and β-hydroxybutyrate levels in males and corticosterone in females both significantly increased with those of HFRs. Results suggest that gulls breeding in densely populated urban environments that are highly exposed to organohalogens may experience perturbations of key hormones involved in energy metabolism leading to metabolic effects.

1. Introduction

Birds living in highly urbanized areas are exposed to a wide range and occasionally high levels of environmental contaminants. Among these are the halogenated flame retardants (HFRs), including polybrominated diphenyl ethers (PBDEs), used to reduce flammability (Covaci et al., 2011) and the per- and polyfluoroalkyl substances (PFAS), used as surfactants (Kucharzyk et al., 2017). Among these, PBDEs, perfluorooctanoic acid (PFOA), and perfluorooctane sulfonate (PFOS) are regulated globally via the Stockholm Convention on Persistent Organic Pollutants (UNEP, 2011, 2017). More recently, perfluorohexane sulfonic acid (PFHxS; 2022) and long-chain perfluorocarboxylic acids (LC-PFCA; 2025) were added to the Convention (UNEP, 2022, 2025). However, several compounds within these chemical families are currently being used and produced in large volumes. A wide range of HFRs, PFAS and other organohalogens persist in the environment and were found to accumulate in the tissues of wild birds, specifically in populations spanning urbanized and densely populated regions (Chen et al., 2012; Gebbink et al., 2011; Gentes et al., 2015). For example, studies on a population of peregrine falcons (*Falco* peregrinus) around the Great Lakes in North America showed greater levels of perfluorinated carboxylic acids (PFCAs) in nestlings (Sun et al., 2020) and BDE-209 (fully brominated BDE congener) in adults from urban areas (Fernie et al., 2017) compared to individuals from rural areas.

Urban-breeding birds therefore may face significant risks from elevated organohalogen exposure, which could disrupt various

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physiological processes potentially leading to adverse health effects (Ortiz-Santaliestra et al., 2019). Notably, these perturbations may stem from the structural similarities of certain HFRs and PFAS with thyroid hormones. Thyroid hormones in vertebrates regulate key functions such as energetic metabolism, thermogenesis, and reproduction (Yavuz et al., 2019). In birds, thyroid hormones are also involved in molting, hatching-related processes, as well as migratory preparation including shifts in lipid metabolism (McNabb, 2007; McNabb and Darras, 2015). Exposure to PBDEs and PFAS has been associated with altered plasma thyroid hormone levels and expression of genes involved in their regulation in certain bird species. For instance, *in ovo* exposure to PFAS in chicken (*Gallus gallus domesticus*) embryos significantly reduced levels of the thyroid hormones triiodothyronine (T_3) and thyroxine (T_4), increased expression of deiodinase type 3 (D3; catalyzing iodine removal), and impaired thyroid gland structure (Mattsson et al., 2019). In ring-billed gulls (*Larus delawarensis*) breeding near the metropolis of Montreal (QC, Canada), liver PBDE concentrations were found to positively correlate with plasma T_4 but negatively correlate with the expression of thyroid-related genes (e.g., thyroid peroxidase and D3), suggesting a potential inhibition of hormone synthesis or signaling (Técher et al., 2016). Similarly, field studies in free-ranging seabirds have reported associations between PFAS and circulating thyroid hormone levels, both in adults (Sebastiano et al., 2021) and in developing chicks (Sebastiano et al., 2023). In addition to thyroid hormones, corticosterone (main glucocorticoid in birds) plays a central role in energy balance. Although less studied, some organohalogens have been associated with altered corticosterone levels in birds. For instance, in Svalbard-breeding black-legged kittiwakes (*Rissa tridactyla*) and glaucous gulls (*Larus hyperboreus*), PFAS and PBDE concentrations were negatively correlated with baseline and stress-induced corticosterone (Tartu et al., 2014; Verboven et al., 2010). These findings suggested disruption of the hypothalamic–pituitary–adrenal (HPA) axis, which supports energetic demands via glycolysis and lipolysis during reproduction or stress (Jimeno and Verhulst, 2023).

Given their role in thermogenesis and lipid metabolism (McNabb, 2007), organohalogens in birds may elicit downstream effects on metabolic processes mediated by disruption of thyroid and glucocorticoid hormone homeostasis. In fact, T_3 regulates resting metabolic rate (RMR) by influencing tissue oxygen consumption and thermogenesis. In thick-billed murres (*Uria lomvia*) from the Canadian Arctic and black-legged kittiwakes from Alaska, T_3 levels were found to strongly correlate with RMR (Elliott et al., 2013; Tremblay et al., 2022). Nonetheless, how thyroid hormones and corticosterone influence daily energy expenditure in wild birds remains unclear. Energy expenditure is influenced by a combination of daily activity budget (e.g., flying, walking, foraging), biological variables (e.g., body condition, age, reproductive status) and environmental factors (e.g., contaminant exposure, weather conditions, food availability), all of which can affect metabolic rates and thermogenesis (Elliott et al., 2013; Dupont et al., 2019). In Svalbard black-legged kittiwakes, body condition and corticosterone levels influenced foraging behaviour and energy allocation, with birds in good body condition increasing their foraging activities under stress, while those in poor condition prioritizing self-maintenance over reproduction (Angelier et al., 2007). Tartu et al. (2014) later reported a positive correlation between plasma perfluorononanoic acid levels and body condition in males from the same kittiwake population. An increased metabolic rate was also observed in Svalbard female black-legged kittiwakes exhibiting greater levels of plasma perfluorotridecanoic acid (Blévin et al., 2017). However, mechanisms through which organohalogens (e.g., HFRs and PFAS) may alter metabolic rates in birds remain unclear, particularly with respect to metabolic processes impacting energy expenditure, lipid metabolism, or energy metabolite production.

Plasma biochemistry also represents a valuable diagnostic tool for assessing physiological disorders and the impact of environmental stressors on wildlife health. For example, plasma biochemical profile was used to evaluate energetic metabolism status including glucose and triglyceride levels in birds exposed to different PBDEs and PFAS (Sonne et al., 2010, 2012). However, despite several studies linking environmental contaminant exposure with changes in metabolic rates and body condition, there is a dearth of studies exploring how anthropogenic stressors (e.g., organohalogens and other contaminants) impact energy metabolite production like glucose, lactate, and ketones in wild birds. Recent work by Millanes et al. (2024) reported positive correlations between plasma glucose and corticosterone levels in spotless starling (*Sturnus unicolor*) chicks, suggesting that glucocorticoids regulate energy metabolism during acute stress, particularly within 15–30 min of exposure to stressors. Moreover, Marteinson and Verreault (2020) investigated the impact of anthropogenic habitat use and exposure to HFRs on the plasma biochemistry (e.g., glucose, calcium, and lactate dehydrogenase) of urban-breeding ring-billed gulls in the Montreal area. Their findings suggested that foraging in anthropogenic habitats and exposure to HFRs may have negative compounding effects on the plasma biochemistry profile of these gulls, potentially leading to health risks of avian wildlife inhabiting highly urbanized environments.

The objective of this study was to assess the linkages between plasma concentrations of PFAS and HFRs, and thyroid hormones and corticosterone involved in energy metabolism, as well as other markers of energy metabolism (plasma biochemistry, energy expenditure) in ring-billed gulls nesting in the highly urbanized and densely populated Montreal area. The ring-billed gull was selected as model species because it is the most abundant gull species in North America, it opportunistically utilizes a wide range of foraging habitats in urbanized regions, and it is exposed to elevated levels of HFRs and PFAS (Chen et al., 2012; Gentes et al., 2012, 2015; Munoz et al., 2022). As such, ring-billed gulls breeding in the Montreal area were found to accumulate high tissue PBDE concentrations due to their frequent foraging in major landfills following exposure through primarily atmospheric emissions in or near these sites (Kerric et al., 2023; Sorais et al., 2021). Earlier studies on the same population reported significant associations between liver PBDE concentrations and plasma thyroid hormone levels (Técher et al., 2016, 2018) and aspartate aminotransferase activity (Marteinson and Verreault, 2020). Certain PBDEs were also reported to positively correlate with field metabolic rate (FMR) in Montreal-breeding ring-billed gull males (Marteinson et al., 2017). Here we hypothesized that higher plasma concentrations of HFRs and PFAS are associated with lower levels of thyroid hormones and corticosterone in breeding ring-billed gulls, particularly in males, and that this results in reduced levels of energetic metabolites and increased energy expenditure. This study offers a novel perspective on the intricate relationships between contaminant exposure and energy metabolism, providing critical insights into the mechanisms of energy metabolism disruption in birds nesting in highly urbanized environments exposed to elevated levels of harmful organohalogens.

2. Materials and methods

2.1. Field sampling

Breeding ring-billed gull females ($n = 41$) and males ($n = 46$) were captured between April and May (i.e., incubation period) 2019, 2022, and 2023 on Deslauriers Island (45.717 °N, 73.433 °W), located 3 km downstream of Montreal (QC, Canada) in the St. Lawrence River. Incubating gulls were captured randomly, one partner per nest, after clutch completion (i.e., three eggs) using either a radio-controlled leg-trap or a dip net. All gulls were equipped with a GPS datalogger coupled to a tri-axial accelerometer (AxyTrek, Technosmart, Guidonia, Italy) affixed at the base of central tail feathers using waterproof tape (TESA, Charlotte, NC, USA). Individuals were tracked for 12 ± 2.4 days (mean ± SEM) in 2019 or 5 ± 0.3 days in 2022 and 2023, during which GPS positions were recorded every 10 min (2019) or 5 min (2022, 2023). After this tracking period, individuals were recaptured for morphometric measurements and tissue collection (see below). The time since clutch completion was determined as the number of days elapsed between the first capture, corresponding to laying of the last egg, and the recapture of the bird.

Following recapture, a first blood sample (up to 3 mL) was collected using a heparinized 25-gauge needle and 10 mL-syringe from the brachial vein within 3 min for corticosterone and other steroid hormone analysis. A second (terminal) sample was then drawn (up to 10 mL) a few min later for thyroid hormone, contaminant, and energetic metabolite analyses. Samples collected in 2019 were used for PFAS analysis exclusively. Body mass and morphometric measurements (wing feather, tarsus and head length, culmen, and beak width) were recorded for all birds. These measures were used to estimate the body condition of birds using the Scaled Mass Index (SMI) following Peig and Green (2009):

$$SMI = M_i \left[\frac{L_0}{L_i}\right]^{b_{sma}}$$

where beak width for females and culmen length for males (i.e., morphometric measurements that were most strongly correlated with the bird's body mass) were used to calculate L_i; M_i represents body mass; L_0 is an arbitrary length measure (beak width or culmen length, depending on sex) calculated as the arithmetic mean of measured values; and b_{sma} is a scaling value obtained by dividing the slope of the linear regression between the length and body mass using Pearson's correlation coefficient (Peig and Green, 2009).

Gulls were then euthanized by cervical dislocation for tissue sampling; the liver was collected in addition to several other tissues that were used as part of companion studies and were kept in a cooler while in the field along with the blood samples. The sex of the birds was determined via gonad examination. In the laboratory, blood samples were centrifuged (2500 x *g*; 7 min) and the resulting plasma was stored in a −80 °C freezer for hormone analysis and in a −30 °C freezer for all other analyses. All capture and handling procedures were approved by the Institutional Committee on Animal Care (CIPA) of the Université du Québec à Montréal (permit no. 960), which complies with guidelines outlined by the Canadian Council on Animal Care (Ottawa, ON, Canada).

2.2. Habitat use characterization

GPS positions from the last 48 h of tracking were retained for each bird to account for the year-specific tracking periods and to better represent plasma variations (i.e., turnover time) of contaminants, energy metabolites, thyroid hormones, and corticosterone. Due to differences in recording intervals for GPS datalogger between some years (5 min *vs* 10 min), we used a fixed 10-min interval for the GPS positions for every gulls. Data were cleaned up by removing data recorded under poor satellite coverage (horizontal dilution of precision > 5). The presence probability of tracked ring-billed gulls was determined based on methods described by Sorais et al. (2020). The Brownian Bridge approach of the Kernel method was used to estimate individual home ranges by taking into consideration the trajectory of the gulls, distinguishing between stopover areas and flying corridors (Horne et al., 2007). The Kernel density estimation was used to determine the foraging areas where the gulls were most likely to be present. The computation of individual home ranges was realized in R 4.4.1 (R Core Team 2024) using the *adehabitatLT* and *adehabitatHR* packages (Calenge, 2006). Among the selected foraging habitats, industrial areas included various industries, airports, quarries and commercial zones, while waste management facilities (WMFs) comprised landfills and wastewater treatment facilities. Waterbodies included the St. Lawrence River, its tributaries, and several nearby lakes. Gulls tracked within the colony as well as those within a 500 m buffer zone around it were excluded such that only the positions associated with foraging activities were kept. The presence probability of gulls in each foraging habitat is detailed in Table S4.

2.3. Overall dynamic body acceleration

Algorithms classifying acceleration measurements into behavioral categories can identify behaviors that are not directly observable in the field (Nathan et al., 2012). GPS dataloggers affixed on ring-billed gulls recorded acceleration along three orthogonal axes (surge, sway, and heave) at a frequency of 10 Hz. For each gull, acceleration data recorded during the last 48 h prior to recapture were cleaned, interpolated, and synchronized to the local time zone. Following the methods described by Sorais et al. (2021), a dataset representing 5-sec acceleration bouts was created, including measurements where at least two consecutive positions were recorded outside of the colony and beyond the 500 m buffer zone (see section 2.2). Behaviors such as feeding, walking, and restricted flight (i.e., short flights within a restricted area) were associated with active foraging. Preening and standing still were grouped together as these activities are associated with minimal energy expenditure. Unrestricted flight was considered separately and identified as high-speed acceleration phase (i.e., free flight). Using classified acceleration measurements from Sorais et al. (2020) as a training set to predict behaviors of free-ranging gulls, the 5-sec bout dataset was then analyzed with the *AcceleRater* tool (Resheff et al., 2014) to categorize behaviors. A random forest model was used to categorize each acceleration pattern to the most likely behavior (e.g., resting, flying, feeding), allowing us to reconstruct the activity budget of each individual from their acceleration patterns. This model was selected because it showed the highest performance in the training set, with 93 % accuracy and 89 % precision. Overall Dynamic Body Acceleration values vary depending on the duration over which the running mean is calculated, typically increasing until they stabilize (Shepard et al., 2008). The running mean is a statistical method used to smooth out short-term fluctuations and highlight longer-term trends in the data. To calculate Overall Dynamic Body Acceleration, we applied this method over 21 different time windows (starting with 0.5 sec, followed by 1 to 20 sec, increasing by 1 sec each time), separately for each individual to account for inter-individual variations in acceleration patterns. The optimal 4-sec window was selected by plotting Overall Dynamic Body Acceleration values over time and identifying the point where the curve reached a plateau, indicating a stable measurement (Shepard et al., 2008). It was then calculated by subtracting the static acceleration to the overall recorded acceleration. The values computed for each individual did not include acceleration during inactive or standing phases as these behaviors were considered static.

2.4. Chemical analyses

2.4.1. HFRs

Plasma samples of ring-billed gulls were analyzed for 34 PBDE congeners and 15 other HFRs (including dechloranes and selected emerging HFRs) at the Université du Québec à Montréal (Montreal, QC, Canada). The full list of compounds is provided in Tables S1 and S2. Sample extraction and clean-up procedures are described in previous studies and were applied without modification (Gentes et al., 2012; Houde et al., 2014). Briefly, an internal standard mixture (BDE-30, BDE-156, ^{13}C-BDE-209, ^{13}C-*anti*-DP; Wellington Laboratories, Guelph, ON, Canada) was added to the homogenized samples, which were solvent-extracted using 1:1 (volume ratio) dichloromethane:*n*-hexanes on a pressurized liquid extraction system (Fluid Management Systems, Billerica, MA, USA). Samples were further cleaned-up with a PBDE-free acid-basic-neutral silica column followed by a PBDE-free neutral alumina column (Fluid Management Systems). Identification and quantification of analytes were conducted using a gas chromatograph coupled to a mass spectrometer (GC–MS) (Agilent Technologies 5975C Series, Palo Alto, CA, USA) operating in electron capture negative ionization mode (ECNI). Method blanks and standard reference material

(SRM) (NIST 1947; Lake Michigan fish tissue, National Institute of Standards and Technology, Gaithersburg, MD, USA) were analyzed in each batch of ten samples. Recoveries (mean ± SD) of internal standards in samples were as follows: BDE-30 (98.3 ± 7.3 %), BDE-156 (96.6 ± 7.9 %), ^{13}C-BDE-209 (59.2 ± 9 %), and ^{13}C-*anti*-DP (91.3 ± 10.4 %). The concentrations of the four PBDE congeners measured in the SRM (n = 4) showed an average variation of 7 % from the certified values. Method limits of detection (MLOD; defined as signal to noise ratio S/N = 3) and method limits of quantification (MLOQ; minimum amount of compound producing a peak with S/N = 10) were established based on replicate analysis (n = 8) of matrix samples spiked at a concentration of 3–5 times the estimated detection limit (Tables S1 and S2).

2.4.1.1. PFAS. A total of 62 PFAS compounds were analyzed in ring-billed gull plasma samples at the Université de Montréal (Montreal, QC, Canada) following methods described by Munoz et al. (2017) with minor modifications. The full list of PFAS compounds is provided in Table S3. For each plasma sample, a 40 μL aliquot was spiked with 120 μL of isotope-labeled internal standards (ILIS) (6 ng/mL in acetonitrile), then 72 μL of methanol and 8 μL of HPLC-grade water were added to induce protein precipitation (Bartolomé et al., 2016). After centrifugation, a 160 μL aliquot of the supernatant was injected onto an ultra-high performance liquid chromatograph (LC) coupled to a high-resolution mass spectrometer (UHPLC-HRMS). Negative and positive ion mode PFAS were acquired in a single 14.5 min run using a polarity-switching heated electrospray ionization source (Martin et al., 2019). A Thermo Hypersil Gold C18 column (100 mm x 2.1 mm, 1.9 μm particle size) was used for analyte separation. To delay potential PFAS contamination to the mobile phase, a Thermo Hypercarb column (20 mm × 2.1 mm, 7 μm particle size) was used as a PFAS trap, and detection was carried out using a Thermo Q-Exactive Orbitrap MS (Waltham, MA, USA) with a scan range of m/z 150–1000 in full scan mode and a resolution of 70,000 FWHM at m/z 200 (Munoz et al., 2022). The QA/QC procedures included analysis of ring-billed gull samples in duplicates, procedural method blanks (HPLC-grade water), and SRM (NIST 1957; Organic Contaminants in Non-Fortified Human Serum, National Institute of Standards and Technology) processed using the same preparation procedures as the gull samples. Among the targeted compounds, four were found in the blanks in 2019 (PFOA mean: 0.007 ng/g plasma equivalent; PFTeDA: 0.002 ng/g; PFHxS: 0.01 ng/g; and PFOS: 0.007 ng/g) and two in 2022–2023 (PFBA: 0.32 ng/g; MeFOSAA: 1.99 ng/g). For those PFAS, levels were blank-corrected and MLODs were derived from the variation in procedural blanks or signal intensity in low-level chicken plasma spikes. MLODs ranged between 0.009 and 44 ng/g plasma equivalent (Table S3).

2.4.1.2. Hormone analysis. Five thyroid hormones (T_3, T_4, rT_3, 3,5-T_2, and 3,3-T_2) along with 27 steroid hormones were analyzed in ring-billed gull plasma at the University of Victoria Genome BC Proteomics Centre (Victoria, BC, Canada) following slightly modified methods described by Jolicoeur et al. (2024). Only T_3 and corticosterone levels were used in the present study. T_3 is the metabolically active thyroid hormone in birds that was found to correlate with metabolic rates (Elliott et al., 2013; Tremblay et al., 2022). Hence, T_3 directly influences tissue oxygen consumption and thermogenesis. Moreover, corticosterone is the main glucocorticoid in birds that is also involved in energetic metabolism. Nevertheless, exploratory analyses showed that the other thyroid hormones (T_4, rT_3, 3,5-T_2, and 3,3-T_2), including their level ratios, did not exhibit significant associations with any of the metabolic endpoints tested, and were therefore excluded from further analyses.

Briefly, plasma samples were mixed with a saturated sodium chloride solution and an IS solution containing ^{13}C or ^{2}H isotope-labeled analogues of 20 steroid hormones, T_3, and T_4 prepared in ethyl-acetate containing 50 μg/mL of butylhydroxytoluene. Samples were then processed through extraction with ethyl acetate. The clear supernatants from the extraction for each calibration solution were pooled and then dried under a nitrogen flow. The dried residues were dissolved in a 40 % acetonitrile solution before analysis. A mixed standard solution of 29 steroid hormones and five thyroid hormones was prepared in the IS solution and serially diluted to create a 9-point calibration solution, with concentrations ranging from 0.0002 to 20 ng/mL. For calibration, 50 μL of aliquoted SigMatrix Ultra Serum Diluent was mixed with 150 μL sodium chloride solution and 400 μL of each calibration solution and then processed similarly to the samples. Analysis was done using an Acquity ultra-performance LC (Waters Corporation, Milford, MA, USA) coupled to a QTRAP 6500 + MS (UPLC-MS/MS) in multiple reactions monitoring (MRM) mode (AB Sciex, Framingham, MA, USA) operated in positive-ion detection mode (ESI +) using 0.05 % formic acid in water and 0.05 % formic acid in acetonitrile as the mobile phase for binary-solvent gradient elution (20 to 80 % over 15 min) at 0.3 mL/min and 55 °C. Results were processed using Sciex OS software. The IS-calibration curves of individual compounds were generated from calibration solution data and analyte concentrations in plasma samples were determined by interpolating these curves using peak area ratios from the sample injections. This UPLC-MS/MS-based quantification method yielded total plasma thyroid hormone levels only (combined bound and free fractions), although we acknowledge that this may represent a limitation with respect to interpreting results in light of potential mechanisms of thyroid disruption.

2.4.1.3. Energetic metabolite analysis. A suite of energetic metabolites was analyzed in ring-billed gull plasma at the Université de Sherbrooke (Sherbrooke, QC, Canada). Only glucose and β-hydroxybutyrate levels were used in the present study. Glucose is the major readily available energy source for birds, while β-hydroxybutyrate is produced when fat stores are mobilized for energy, indicating a shift in the primary energy source under stress or fasting.

Briefly, plasma samples (10–50 mg) were homogenized on ice, spiked with an IS solution (γ-aminobutyric acid-d6 and ^{13}C-glucose) and treated with 500 μL of 0.4 M perchloric acid containing 5.5 mM ethylene glycol-*bis*(β-aminoethyl)-N,N,N',N'-tetraacetic Acid (EGTA). After vortexing and centrifugation (14,000 x *g*, 4 °C, 10 min), the supernatant was neutralized with 135 μL of 0.5 M potassium carbonate (K_2CO_3), centrifuged once more (14,000 x *g*, 4 °C, 30 min), and then filtered through a 0.2 μm regenerated cellulose syringe filter. Analyte separation was achieved on a HILIC-Z column (2.1 × 100 mm, 2.7 μm particle size) using a UPLC-MS/MS consisting of an ACQUITY Xevo TQ MS system (Waters Corporation, Milford, MA, USA) coupled with an ACQUITY Binary Solvent Manager (Waters Corporation). The flow rate was 400 μL/min and the column temperature was set to 40 °C. Mobile phases consisted of water (mobile phase A) and acetonitrile/water (85:15; volume ratio) (mobile phase B) with 10 mM ammonium acetate (pH 9). The MS analysis used ESI + and ESI- in MRM mode with two product ion transitions monitored for each analyte. The most abundant ion was used for quantification, while the second most abundant ion was used for identification. Data were processed using MassLynx V4.2 software (Waters Corporation).

2.5. Statistical analyses

2.5.0.1. Effects of foraging habitat use on contaminant concentrations

We used linear mixed-effect models to evaluate the relationships between the concentrations of $\sum_{62}$PFAS and $\sum_{49}$HFR in gull plasma and foraging habitats used by ring-billed gull males and females. Among the targeted HFRs and PFAS, only individual compounds with a detection frequency (i.e., > MLOD) above 60 % were included in the analyses (Tables S1-S3). For all statistical analyses using HFRs, $\sum_{34}$PBDE, the sum of the two DP isomers *anti*- and *syn*-DP ($\sum_2$DP), and hexabromobenzene (HBB) were considered. PFAS were evaluated as summed concentrations of perfluorinated carboxylic acids (Σ_{11}PFCA) and perfluorinated sulfonic acids (Σ_9PFSA).

Due to potential differences in feeding ecology and energy expenditure between ring-billed gull males and females during the breeding season, we included sex as an explanatory variable in the analyses. Sampling year (2019, 2022, or 2023) was included as a random effect in the PFAS models. For the HFR models, only two years were used because data for other variables (except for gull GPS positions) were not available in 2019, and sampling year was therefore included as a fixed effect. We then formulated a set of 11 candidate models that could potentially explain the concentrations of $\sum_{49}$HFR or $\sum_{62}$PFAS in gull plasma samples based on biological hypotheses (Table S7). Concentrations of $\sum_{49}$HFR and $\sum_{62}$PFAS were log-transformed to meet the assumptions of homoscedasticity and normality of residuals. We evaluated the candidate models using Akaike's information criterion corrected for small sample size (AIC_c) using the *AICcmodavg* package in R 4.4.1 (Burnham and Anderson, 2002; Mazerolle, 2023). A multimodel inference approach was used to assess the effects of explanatory variables and predict the concentrations of organohalogens using the shrinkage estimator for model averaging (Burnham and Anderson, 2002).

2.5.0.2. Relationships between organohalogens, hormones, body condition, and energy metabolism markers

We developed a theoretical model to describe the relationships between PFAS or HFRs and hormones, energetic metabolites, Overall Dynamic Body Acceleration, and SMI in ring-billed gulls. To estimate these relationships, we formulated a structural equation model that included all components of the theorical model for a given compound (HFRs or PFAS) for gulls sampled in 2022 and 2023 (Grace et al., 2010; Fig. 1). This model allowed us to simultaneously examine direct and indirect effects within a hypothesized network of relationships. We analyzed data separately for males and females to account for potential sex-specific differences in the underlying physiological pathways linking exposure and metabolism. Furthermore, HFRs and PFAS were each summed into $\sum_{49}$HFR and $\sum_{62}$PFAS concentrations. The model also incorporated the time since clutch completion due to its influence on body reserve fluctuations in females post egg-laying (Vézina and Williams, 2003). Each component *i* (e.g., $\sum_{49}$HFR, $\sum_{62}$PFAS, T_3, corticosterone, β-hydroxybutyrate, SMI, glucose, Overall Dynamic Body Acceleration, and time since clutch completion) for a bird *j* of a given sex was log-transformed and modeled using a normal distribution:

$$logY_{ij} \sim N\left(\mu_{ij}, \sigma_i^2\right)$$

$$\mu_{ij} = X_{ij}\beta_i$$

where μ_{ij} denotes the logarithmic concentration of component *i* for bird *j*; and σ_i^2 represents the residual variance associated with this component. The regression model for each component *i* corresponds to the product of the design matrix X_{ij} and a vector of coefficient β_i, which characterizes how component *i* relates to the explanatory variables. The design matrix X_{ij} included terms for the intercept as well as the explanatory variables relevant to component *i* (Fig. 1). Each coefficient in β_i quantifies the influence of a specific explanatory variable on the response. Structural equation models were fit using maximum likelihood estimation with the *lavaan* package in R 4.4.1 (R Core Team, 2024; Rosseel, 2012). We used residual diagnostics to ensure that assumptions of homoscedasticity and normality for the different regression components were met.

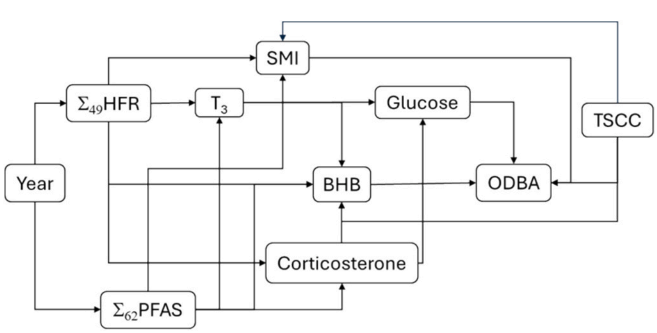

Fig. 1. Theoretical structural equation model of HFR and PFAS exposure-related effects on hormone regulation and energy metabolism in Montreal-breeding male and female ring-billed gulls. Boxes at the base of each arrow represent explanatory variables that may influence the response variable at the arrow's endpoint. SMI: Scaled Mass Index; BHB: β-hydroxybutyrate; ODBA: Overall Dynamic Body Acceleration; TSCC: Time since clutch completion.

3. Results

3.1. Factors influencing organohalogen concentrations

Concentrations of $\sum_{49}$HFR and $\sum_{62}$PFAS determined in ring-billed gull plasma are detailed in Tables S8 and S9. Among HFRs, $\sum_{34}$PBDE were the most abundant (98 % of $\sum_{49}$HFR), while PFOS was the most abundant PFAS both in terms of concentrations (mean ± SEM: 73.1 ± 8.4 ng/g ww) and relative contributions (70 % of $\sum_{62}$PFAS). The most parsimonious models explaining the concentrations of Σ_{34}PBDE in ring-billed gulls included the presence probability of gulls in WMFs, with an Akaike weight of 57 %. The second-best model, which also included sex, had a weight of 22 % (Table 1). However, shrinkage estimates indicated that neither the presence in WMFs nor sex influenced concentrations of Σ_{34}PBDE, as the 95 % confidence intervals overlapped zero (Table S10). For $\sum_2$DP and HBB, the null model (intercept only) scored as the most parsimonious model ($\Delta AIC_c = 0$, $w = 0.24$ and $\Delta AIC_c = 0$, $w = 0.23$), indicating that none of the tested variables explained the variations of these two HFRs. Multimodel inference did not show an effect of any other foraging habitats on HFR concentrations (Table S10).

For PFAS, the top-ranking model for $\sum_{11}$PFCA, including the presence probability of gulls in industrial areas, yielded moderate support with an Akaike weight of 35 % (Table 2). However, the null model followed closely with an Akaike weight of 17 %, suggesting that the added explanatory value of the presence of gulls in industrial areas was limited. Shrinkage estimates supported this result as $\sum_{11}$PFCA did not vary with their presence in industrial areas (Table S11). For $\sum_9$PFSA, the most parsimonious models explaining their concentrations included the presence probability of gulls in industrial areas, with an Akaike weight of 35 % for the top-ranking model and a weight of 23 % for the model including sex (Table 2). Shrinkage estimates, however, suggested that $\sum_9$PFSA concentrations did not vary with either the presence in industrial areas or sex of the gulls as their 95 % confidence intervals included zero (Table S11). Plasma organohalogen concentrations generally did not vary between sexes (Tables S10 and S11).

Table 1
Results of model selection ($\Delta AIC_c < 2$) among linear mixed models explaining the concentrations (*C)* of HFRs in plasma of 60 ring-billed gulls breeding in the Montreal area (QC, Canada) in 2022 and 2023. Explanatory variables included the presence probability of gulls in different foraging habitats (Presence) including sex and year as fixed effects. WMFs: Waste Management Facilities.

Model	*K*	AIC_c	ΔAIC_c	*w*
$\sum_{34}$PBDE				
C ~ $Presence_{WMFs}$	4	109.23	0.00	0.57
C ~ $Presence_{WMFs}$ + Sex	5	111.10	1.88	0.22
$\sum_2$DP				
C ~ Intercept	3	117.90	0.00	0.24
HBB				
C ~ Intercept	3	138.90	0.00	0.23

Table 2
Results of model selection ($\Delta AIC_c < 2$) among linear mixed models explaining the concentrations (*C)* of PFAS in plasma of 87 ring-billed gulls breeding in the Montreal area (QC, Canada) in 2019, 2022, and 2023. Explanatory variables included the presence probability of gulls in different foraging habitats (Presence) including sex as a fixed effect and year as a random effect.

Model	*K*	AIC_c	ΔAIC_c	*w*
$\sum_{11}$PFCA				
C ~ $Presence_{industrial}$	4	130.32	0.00	0.35
C ~ Intercept	3	131.78	1.45	0.17
$\sum_{9}$PFSA				
C ~ $Presence_{industrial}$	4	197.29	0.00	0.35
C ~ $Presence_{industrial}$ + sex	5	198.17	0.89	0.23

3.2. Relationships between organohalogens, hormones, body condition, energetic metabolites, and overall dynamic body acceleration

The structural equation models revealed sex-specific associations in ring-billed gulls between HFRs or PFAS, and thyroid hormones, corticosterone, and energetic metabolites (Tables S12 and S13; Fig. 2). For males, plasma T_3 and β-hydroxybutyrate levels (Tables S5 and S6) increased with concentrations of $\sum_{49}$HFR (Figs. 2 and 3). Additionally, glucose levels (Table S6) in males increased with plasma T_3 levels. Furthermore, β-hydroxybutyrate levels in males decreased with $\sum_{62}$PFAS concentrations, with a similar trend observed for T_3 levels (Figs. 2 and 3). Moreover, levels of β-hydroxybutyrate decreased with time since clutch completion for males, although this effect was marginal (90 % CI excluded 0) (Fig. 2). In females, corticosterone levels (Table S5) increased with $\sum_{49}$HFR concentrations (Fig. 2). In contrast to results for males, β-hydroxybutyrate levels in females increased with $\sum_{62}$PFAS concentrations (Figs. 2 and 3). Lastly, Overall Dynamic Body Acceleration in females increased marginally with SMI (90 % CI excluded 0) (Fig. 2). The year did not have any effect on organohalogen concentrations in either sex.

4. Discussion

4.1. Sources of organohalogen exposure

Overall, predictors related to foraging habitat use on plasma HFR and PFAS concentrations in Montreal-breeding ring-billed gulls showed weak support and the uncertainty around their effects was notable. Although the top-ranked models for plasma PBDE concentrations included the presence of gulls in WMFs, we found no significant association between these two variables. Previous studies reported that ring-billed gulls foraging in landfills and wastewater treatment plant aeration ponds exhibited higher plasma PBDE concentrations, with air and dust likely representing the main exposure route (Gentes et al., 2015; Sorais et al., 2020; Kerric et al., 2023). However, over the past decade, PBDE concentrations in gulls from the Great Lakes and St. Lawrence regions have shown a general decline. For example, Σ_{14}PBDE concentrations in herring gull (*Larus argentatus*) eggs declined by 33 % between 2006 and 2012 (Su et al., 2015) and plasma penta-BDE concentrations decreased by 5.7 % per year between 2010 and 2021 (Brady et al., 2024). These

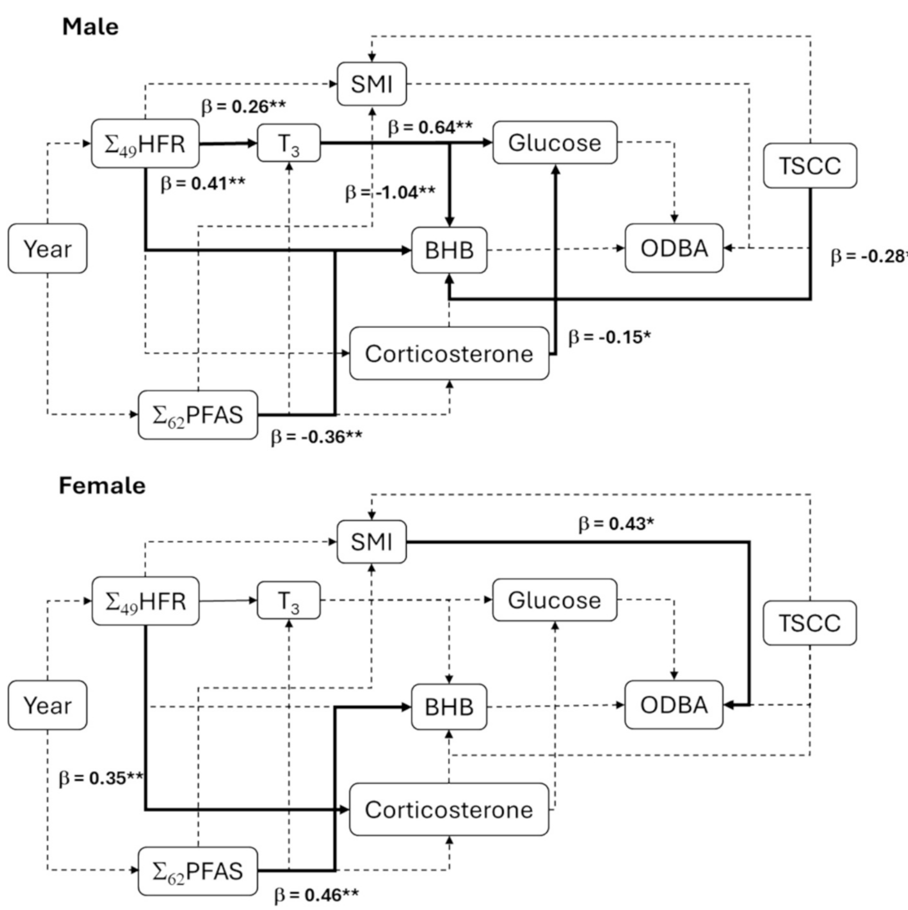

Fig. 2. Path analysis of HFR and PFAS, hormone and metabolic marker levels inferred from structural equation models for male and female ring-billed gulls breeding in the Montreal area (QC, Canada). The values above the bold arrows represent the regression coefficients (β) on a log scale that describe the influence of explanatory variables on response variables when significantly different from 0. Dashed line arrows correspond to the absence of influence of one variable on another. Estimates marked with one asterisk (*) indicate a 90% confidence interval (CI) excluding 0, while those with two asterisks (**) indicate a 95% CI excluding 0. SMI: Scaled Mass Index; BHB: β-hydroxybutyrate; ODBA: Overall Dynamic Body Acceleration; TSCC: Time since clutch completion.

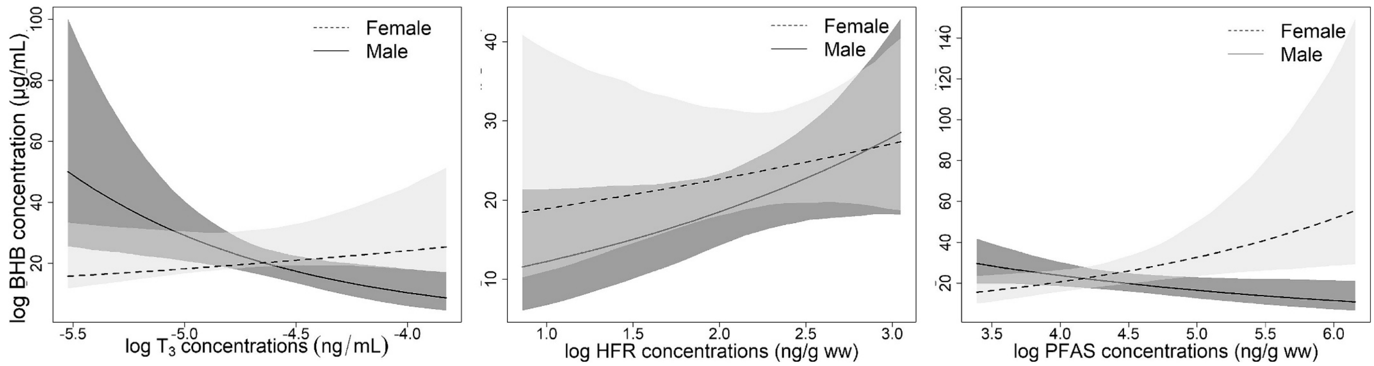

Fig. 3. Estimated plasma β-hydroxybutyrate (BHB) levels based on those of T_3 or organohalogens in ring-billed gulls breeding in the Montreal area (QC, Canada). Predicted BHB concentrations (log µg/mL) are shown as a function of T_3 concentrations (log ng/mL), $\sum_{49}$HFR concentrations (log ng/g ww), and $\sum_{62}$PFAS concentrations (log ng/g ww). Separate predictions with shaded grey areas representing 95% confidence intervals are provided for females (dotted lines, light grey area) and males (solid lines, dark grey area).

temporal trends in gulls from the Great Lakes region over the last two decades likely occurred in ring-billed gulls from the Montreal area in the adjacent St. Lawrence basin. This could explain, at least in part, the absence of relationships between plasma HFR concentrations in ring-billed gulls and the time spent in any foraging habitats. As such, a two-point comparison in plasma PBDE concentrations in this ring-billed gull colony (Deslauriers Island) between the Gentes et al. (2015) study (2010–2012 samples; April-May) and our study (2022–2023 samples; April-May) aligns well with these trends. Specifically, mean plasma $\sum_{34}$PBDE concentrations in 2022–2023 were approximately 3.8-fold lower in males and 2.2-fold lower in females compared to 2010–2012, which was consistent with the reported regional trends. Further investigation of temporal changes in PBDE concentrations in ring-billed gulls within this area would be required to corroborate these findings.

This study provides a comprehensive analysis of PFAS concentrations in Montreal-breeding ring-billed gulls, highlighting the importance of highly urbanized environments as significant sources of exposure for certain urban-adapted avian species. However, PFAS concentrations in present ring-billed gull plasma were in the lower range of those reported for gulls elsewhere. For example, median plasma concentrations of $\sum$PFAS in Montreal ring-billed gulls were 1.8-fold lower compared to the highest median concentration reported in plasma of herring gulls from the Great Lakes (Brady et al., 2024). Following the same pattern as HFRs, plasma ΣPFAS concentrations in Great Lakes herring gulls declined by approximately 7.7 % per year between 2010 and 2019, with $\sum$PFSA decreasing slightly faster (9.7 %; Brady et al., 2024). Egg monitoring studies generally support these trends, revealing decreasing PFAS concentrations (especially for PFOS) in herring gull eggs across the Great Lakes between 1990 and 2010. Interestingly, PFCA concentrations tended to rise over time in herring gulls from the most urbanized areas like the Toronto Harbour (ON, Canada) (Gebbink et al., 2011; Letcher et al., 2015).

Among all models considered, the ones including the presence of ring-billed gulls in industrial areas received the strongest support based on model selection. However, the effect size was small, and the intercept-only model received nearly equivalent support, indicating a very weak explanatory power overall. This suggests that while industrial areas may represent a source of PFCA exposure in Montreal-breeding ring-billed gulls, the data do not provide robust evidence for a consistent effect. As for $\sum$PFSA, while the presence of gulls in industrial areas also was retained in the top-ranked models, the lack of statistical support and high uncertainty around its effect suggested it is not a strong predictor in ring-billed gull plasma. Extensive industrial use has made PFAS ubiquitous, although the specific sources within Montreal's industrial areas remain undocumented. Industrial sectors in the greater Montreal including textile manufacturing, construction, and aeronautics (Lacourt et al., 2015; Liu et al., 2021; Shafiee Roudbari et al., 2024) are known PFAS sources, and thus may contribute to their local exposure (Janousek et al., 2019; Liu et al., 2021). Recent studies have highlighted the widespread occurrence of PFAS in the St. Lawrence region, being detected in water, sediments, and various aquatic organisms (Munoz et al., 2022). To date, no studies have investigated specific sources of PFAS exposure for gulls or any other bird species in the Montreal area or in the St. Lawrence River.

Our results align well with studies reporting higher PFCA and PFSA concentrations in herring gull eggs near urbanized or industrialized areas in the Canadian provinces of Ontario and Quebec (Gebbink et al., 2011; Letcher et al., 2015). Similar patterns have also been reported internationally. In Australia, PFAS concentrations in little penguins' blood increased with urbanization (Wells et al., 2024) and in Europe, very high PFOS concentrations were documented in great tits and their eggs, as well as in Mediterranean gull eggs near an industrial area, with concentrations declining with distance but remaining elevated up to 10 km (Groffen et al., 2017; Lopez-Antia et al., 2017). While no single habitat strongly predicted PFAS concentrations in plasma of present ring-billed gulls, their omnivorous and opportunistic foraging behavior likely led to exposure from multiple diffuse sources in this heterogeneous urban landscape.

Concentrations of HFRs and PFAS were expected to vary between ring-billed gull males and females primarily due to maternal transfer as individuals were all sampled for blood shortly after egg laying. However, no sex-specific difference was observed for either HFRs or PFAS. We similarly found no sex-specific differences in foraging habitat use strategy between gull males and females, except for females that generally spent slightly more time in agricultural fields. Although females are known to transfer part of their organohalogen burden to their eggs (e.g., Knudtzon et al., 2021), comparable HFR and PFAS concentrations among males and females shortly after egg laying may suggest stronger retention of certain compounds in females due to plasma protein binding. For example, higher concentrations of heavy rare earth elements such as Yttrium in ring-billed gull females compared to males from this same colony were suggested to be due, at least in part, to binding to plasma proteins (e.g., albumin, transthyretin) (Brown et al., 2019). Indeed, a study on American kestrels (*Falco sparverius*) showed that females have higher total plasma protein content than males during the pre-laying and incubation periods (Dawson and Bortolotti, 1997). It was previously reported that PFAS effectively bind to serum albumin, affecting its structure and potentially interfering with its normal function (Jones et al., 2003; Starnes et al., 2024). Similarly, certain PBDEs were shown to competitively bind to both serum albumin and transthyretin in herring gulls (Ucán-Marin et al., 2010). Additional research is needed to explore how bioavailable PFAS interacts with plasma proteins in female birds and how this may influence the transport and availability of essential macromolecules in the bloodstream.

4.2. Influence of organohalogens on T_3 and corticosterone

The present study revealed a positive influence of plasma ∑HFR concentrations on total T_3 levels in Montreal-breeding ring-billed gull males, whereas no such influence was found in females. Previous studies, both in the laboratory and in the field, highlighted that while a range of HFRs (e.g., PBDEs, hexabromocyclododecane) were associated with perturbed thyroid functions, the avian thyroid system is moderately sensitive to these organohalogens and highly species-specific (reviewed by Guigueno and Fernie (2017)). For instance, Fernie and Marteinson (2016) reported a decrease in T_3 levels in captive female American kestrels experimentally exposed to a penta-BDE mixture (DE-71) via the diet. However, a study on free-ranging peregrine falcon nestlings from the Great Lakes showed no significant relationship between T_3 levels and ∑PBDE concentrations, despite large regional differences (Smits and Fernie, 2013). Técher et al. (2018) further reported a similar lack of relationship between PBDE levels and those of T_3 in developing ring-billed gull embryos from the same Montreal colony and a colony located further east near Quebec City, Canada (Bellechasse Island). Additionally, Marteinson and Verreault (2020) did not observe any correlation between HFRs (PBDEs, dechlorane-related compounds) and free and total T_3 and T_4 in breeding ring-billed gulls from this Montreal-based colony sampled in 2011–2012.

No association was observed between PFAS and T_3 levels in either sex. As reported for HFRs, the effects of PFAS on thyroid hormones in birds are highly inconsistent across species and life stages. While PFAS concentrations have been associated with those of T_4 in a few raptor and gull species (e.g., Ask et al., 2021; Sebastiano et al., 2021; Sun et al., 2021), no association with T_3 was found in Svalbard kittiwakes (Nøst et al., 2012). In present study, PFAS may have affected thyroid functions by disrupting T_4 levels or T_4 to T_3 conversion through deiodinases, with comparatively weaker effects on circulating T_3 (Mattsson et al., 2019; Sun et al., 2021). One proposed mechanism is that PFAS may compete with thyroid hormones for binding to plasma proteins (e.g., albumin, transthyretin). Because most circulating T_4 and T_3 are bound to albumin and transthyretin in birds, which can also occur for PFAS, positive correlations between PFAS and T_3 may partially reflect variations in plasma protein content (Ask et al., 2021, McNabb, 2007). Measuring the free thyroid hormone fraction, which our UPLC-MS/MS-based quantification method did not allow, would perhaps clarify whether observed associations were due to plasma PFAS-protein interaction. The absence of influence on T_3 levels does not exclude PFAS-mediated effects on thyroid hormone regulation, as effects may be more pronounced on levels of T_4, T_4/T_3 conversion (i.e., iodine removal through deiodinases), or on the free fraction of T_3. In contrast, ∑HFR positively influenced corticosterone levels in present ring-billed gull females, but not in males, which may suggest a sex-specific response. The limited number of studies investigating the impact of HFRs on corticosterone regulation in wild birds have shown varying responses depending on the tissue and species examined. For instance, exposure to PBDEs was associated with decreased feather corticosterone levels in Svalbard great skuas (*Stercorarius skua*) (Bourgeon et al., 2012) or an increase in baseline plasma corticosterone levels in Svalbard glaucous gulls (Verboven et al., 2010). The influence of HFR exposure on corticosterone could result from upstream effects in the hypothalamus–pituitary–adrenal axis or immune functions (Fernie et al., 2005). Indeed, certain organohalogens may interfere with glucocorticoid receptors or hormone synthesis pathways (Odermatt et al., 2006), leading to dysregulation of corticosterone synthesis or metabolism.

4.3. Influence of organohalogens on β-hydroxybutyrate

Contrasting relationships between β-hydroxybutyrate levels and those of ΣHFR and ΣPFAS were observed in male ring-billed gulls. Specifically, ∑HFR concentrations had a moderate positive influence on β-hydroxybutyrate levels in males only, which may reflect a contaminant-induced shift in energy mobilization through lipid oxidation. Ketone bodies, which include β-hydroxybutyrate, are lipid-derived metabolites produced via hepatic fatty acid oxidation (i.e., ketogenesis). They represent key circulating energy sources during enhanced lipid mobilization, especially under metabolic stress when glucose availability is low (Newman and Verdin, 2014). In birds, β-hydroxybutyrate has frequently been used as a marker of lipid metabolism, with elevated levels reflecting increased lipid mobilization during metabolic stress such as fasting, prolonged flight, and rapid body mass changes (Bairlein et al., 2015; Cerasale and Guglielmo, 2006). These findings may reflect a regulatory shift in fatty acid oxidation pathways in response to HFR exposure in present ring-billed gulls, potentially influencing lipid mobilization. HFR exposure was reported to disrupt fatty acid metabolism and cholesterol regulation, for instance, by altering the expression of peroxisome proliferator activated receptors (PPARs), fatty acid-binding proteins, and enzymes such as CYP7B1 and 3-Hydroxy-3-methylglutaryl-CoA reductase (HMGCR) in American kestrel hatchlings (Goodchild et al., 2022).

In contrast, β-hydroxybutyrate levels decreased with increasing ∑PFAS concentrations in male ring-billed gulls, suggesting a potential inhibition of ketogenesis. This may involve alteration in enzymes responsible for lipid oxidation or in the transcription of genes regulating lipid mobilization. Specifically, PPARs and certain CYP isoenzymes (e.g., CYP4A, CYP2E1) are key players in fatty acid oxidation and detoxification of lipid-derived metabolites and are essential for ketogenesis. Disruption of their functions could reduce lipid oxidation and β-hydroxybutyrate formation. For instance, juvenile chickens exposed to different concentrations of PFOA or PFOS in the laboratory resulted in decreased expression of genes involved in lipid and fatty acid metabolism such as carnitine palmitoyltransferase 1A (CPT1A), a key enzyme in fatty acid oxidation as well as HMGCR (Yeung et al., 2007).

In contrast, ∑PFAS had a positive influence on β-hydroxybutyrate levels in ring-billed gull females, rather suggesting an enhanced lipid mobilization, potentially through increased fatty acid oxidation or upregulation of genes involved in ketogenesis in response to PFAS exposure. This contrasting response between male and female ring-billed gulls may reflect sex-specific regulation of metabolic pathways including differences in the expression or activity of genes involved in ketogenesis. These differences may be partly explained by the inherent physiological differences in metabolic demands associated with reproduction in precocial birds. For instance, genes involved in lipid metabolism such as lipoprotein lipase in chicken during sexual maturation were upregulated in ovaries to support greater lipid mobilization and steroidogenesis required for oocyte development (Cui et al., 2022). These metabolic pathways, which are more active or sensitive in females, may render them more responsive to PFAS-induced metabolic disruption. Additionally, estrogens can also modulate liver lipid regulation through estrogen receptor upregulation of the expression of lipid-related proteins, thus promoting lipid export and preventing excess lipid accumulation (Deng et al., 2022). These mechanisms may underly the higher β-hydroxybutyrate levels uncovered in females as they support enhanced lipid mobilization and ketogenesis under putative contaminant-induced metabolic stress.

The effects of PFAS exposure or dosage on lipid metabolism are unclear as there appears to be conflicting evidence about their impact on genes involved in lipid regulation as both up- and down-regulation of genes were reported (Jacobsen et al., 2018). For example, Jacobsen et al. (2018) observed a downregulation of several genes involved in fatty acid metabolism including carnitine palmitoyltransferase 2 (CPT2) and acetyl-CoA acetyltransferase 1 (ACAT1) in liver of chicken embryos exposed *in ovo* to PFOS. In their study, the most affected pathway was the metabolism regulating mitochondrial energy production, lipogenesis and fatty acid oxidation, with short chain fatty acids (e.g., butyrate) acting as a switch between fatty acid oxidation and lipogenesis (Jacobsen et al., 2018). However, several other studies reported opposite effects on these metabolic pathways. In the present study, the divergent relationships between ΣPFAS and β-hydroxybutyrate levels in ring-billed gull males and females highlight the complexity of PFAS-induced metabolic disruption and underscore the need for further investigation into the molecular mechanisms underlying these observations.

4.4. Linkages between hormones, body condition, and energetic metabolites

The positive association between plasma T_3 concentrations and glucose levels in male ring-billed gulls may support, at least in part, the role of thyroid hormones in regulating circulating glucose levels. This could occur not only by increasing energy production via gluconeogenesis, but also by enhancing glucose uptake through its interaction with membrane proteins like Ca^{2+}-ATPase, adenylate cyclase, and glucose transporters (Decuypere et al., 2005). However, plasma glucose levels are regulated by various factors and the absence of such correlation in females may again suggest that other mechanisms might be at play to regulate glucose levels such as glucocorticoids or insulin. For instance, glucocorticoids regulate glucose synthesis by promoting gluconeogenesis in the liver, making it available for immediate energy demands (Jimeno and Verhulst, 2023; Taff et al., 2022), while insulin contributes to the regulation of blood glucose in birds (reviewed by Sweazea (2022)).

The concentrations of β-hydroxybutyrate were also found to decrease with increasing T_3 levels in male ring-billed gulls. As such, glucose and β-hydroxybutyrate act as antagonists, as β-hydroxybutyrate concentrations increase during lipid oxidation for energy production under periods of low glucose availability in plasma. Moreover, β-hydroxybutyrate levels tended to decrease in ring-billed gull males with increasing time since clutch completion. This pattern suggested a decrease in the use of ketone bodies over time in males since the last egg was laid. During the incubation period, ring-billed gulls spent the majority of their time (~80 %) attending the nest, and males spent significantly more time in this activity than females shortly after egg laying. This increased nest site attentiveness may limit foraging opportunities, potentially leading to reduced food intake and a greater reliance on lipid reserves to meet energetic demands. In contrast, the lack of influence of time since clutch completion on plasma β-hydroxybutyrate levels in females might be explained by the higher energy spent during egg-laying that was offset by greater food consumption during this same period to recover for endogenous body resource loss. The negative and marginal influence of corticosterone on glucose levels in male ring-billed gulls also emphasized the role of this hormone in regulating plasma glucose levels (Jimeno and Verhulst, 2023; Taff et al., 2022). The weak influence of corticosterone or the lack of an effect in females support that other physiological or environmental variables may be more important than corticosterone in controlling glucose levels in gulls.

Finally, although the positive influence of SMI on Overall Dynamic Body Acceleration in ring-billed gull females was marginal, it suggested that females in better body condition were more active, engaging more frequently in energetically costly behaviors such as foraging, walking or flying. These findings further support that females were more actively foraging post-egg laying than males to replenish their lost energy reserves. Nonetheless, using Overall Dynamic Body Acceleration as a proxy for energy expenditure has limitations as it does not consider external factors like temperature and weather conditions, which can affect an individual's metabolic needs. Energy expenditure is not solely driven by movements as it also depends on basal metabolic processes and should account for resting costs, including those related to thermoregulation during incubation (Tremblay et al., 2022).

4.5. Conclusions

Present study provides new insights into the complex interactions between organohalogen contaminant exposure, endocrine regulation, and energy metabolism in an urban-adapted gull population. Plasma HFR and PFAS concentrations in ring-billed gulls were not associated with the use of specific foraging habitats, likely reflecting the generalist foraging behavior of ring-billed gulls and the diffuse sources of organohalogens in this heterogenous urbanized landscape. Additionally, we identified sex-specific differences in endocrine and metabolic responses, suggesting a potential organohalogen-related physiological disruption of lipid metabolism. In males, HFRs were positively associated with T_3 and β-hydroxybutyrate levels, whereas PFAS were linked to decreased β-hydroxybutyrate levels. In contrast, females showed increased corticosterone levels in response to HFRs and elevated β-hydroxybutyrate levels with increasing PFAS exposure. These findings suggest that organohalogens may alter lipid metabolism through hormone-mediated mechanisms in a sex-specific manner. Our results underscore the relevance of metabolic biomarkers such as β-hydroxybutyrate in ecotoxicological studies and have important implications for birds nesting and feeding in and around highly urbanized areas. Finally, while our study revealed sex-specific metabolic responses, this was not reflected by changes in Overall Dynamic Body Acceleration. This finding suggests that Overall Dynamic Body Acceleration may not fully capture changes in metabolic processes that contribute to energy use beyond foraging movements alone and would warrant further research by integrating environmental and ecological factors.

CRediT authorship contribution statement

Coralie Turquois: Writing – original draft, Methodology, Investigation, Formal analysis. **Marc J. Mazerolle:** Writing – review & editing, Methodology. **Sébastien Sauvé:** Writing – review & editing, Methodology. **Lounès Haroune:** Writing – review & editing, Methodology. **Jonathan Verreault:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envint.2025.110012.

Data availability

Data will be made available on request.

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