

Repeated measures of mercury concentrations demonstrate persistent territory-level contamination and stable individual differences in exposure in a riverine bird predator

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Abstract

Mercury is a persistent, toxic metal that bioaccumulates and biomagnifies in food webs, causing lethal and sublethal effects in wildlife even at low concentrations. It poses a pervasive threat to aquatic ecosystems through transformation into the highly toxic and bioavailable form, methylmercury. Yet the relative contributions of environmental and individual sources to variation in mercury exposure in wild populations remain unclear. We quantified total mercury concentration in feathers of adult female white-throated dippers (*Cinclus cinclus*) breeding along 11 rivers in the Chartreuse mountains, France, differing in anthropogenic pressures. Using 777 feathers from 451 adult females sampled up to three times from 2017 to 2025, we conducted repeatability analyses and linear mixed models to test the influence of landscape features on mercury exposure. Feather mercury averaged $1.62 \pm 0.95 \text{ mg}\cdot\text{kg}^{-1}$, with 0.8% of samples exceeding the $5 \text{ mg}\cdot\text{kg}^{-1}$ toxicity threshold. When modelled separately, individual identity explained 80% of variance in mercury, territory identity explained 53%, and river identity explained 31%. When modelled together, variance was redistributed, with individual identity explaining 42% of variance in mercury, followed by river (26%) and territory (12%). Contrary to expectations, mercury was negatively associated with human footprint index. As white-throated dippers are highly faithful to their territory across years, our results suggest mercury exposure is shaped by persistent territory-level contamination and stable individual differences, with territory effects likely reflecting legacy contamination. These findings underscore the value of repeated sampling of known individuals and integrating human impact gradients to assess contaminant exposure risks in natural populations.

Introduction

Chemical pollutants are nowadays widely encountered in wild ecosystems, which can pose substantial challenges to wildlife health and ecological integrity. These substances include both natural elements, such as mercury, which can reach harmful concentrations through human activities (Selin, 2009), and synthetic compounds specifically of anthropogenic origin, such as persistent organic contaminants (Aladl et al., 2025). Chemical pollution has become a major global concern due to the persistence and bioaccumulation of many substances, including legacy pollutants such as metal trace elements (MTEs), organic pollutants such as dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs), and emerging pollutants such as per- and polyfluoroalkyl substances (PFAS) (Li et al., 2024). Despite decades of research, substantial knowledge gaps remain in understanding the origin of between-individual variation in exposure to and accumulation of chemical pollutants, and to what extent such variation is driven by environmental (Chatelain et al., 2021) or individual (e.g., genetic; Bertram et al., 2024b) factors. Understanding these sources of variation matters beyond exposure itself: it is a prerequisite for assessing the short- and long-term effects of pollution on individual fitness and, potentially, selection for strategies that allow individuals or populations to cope with the selective pressures chemical pollutants impose. Such effects may be subtle, only becoming measurable after prolonged or multigenerational exposure (Wolfe et al., 1998; Heinz, 1979).

Among pollutants, mercury is of particular interest because of its ubiquity: it is both naturally occurring and globally dispersed through anthropogenic activities, yet its ecological effects are strongly context dependent. Mercury, like most MTEs, is naturally present in the earth's crust and is therefore expected to be found at low concentrations in all organisms (Kalisinska, 2019). Over the past centuries, anthropogenic activities such as fossil fuel combustion, mining, waste incineration, and industrial processes have greatly increased environmental mercury loads and altered its cycling (Selin, 2009). In the environment, mercury undergoes transformation by microorganisms into its most toxic organic form, methylmercury, which is highly bioavailable and persistent (Selin, 2009; Hsu-Kimet al., 2013). Methylmercury bioaccumulates and biomagnifies along food webs, so that even low aqueous concentrations can generate substantial body burdens in higher-trophic-level consumers such as predatory birds and mammals (Cristol et al., 2008; Rimmer et al., 2010; Wolfe et al., 1998). In particular, aquatic environments, which often act as sinks for mercury and many other chemical pollutants through water runoff, can expose resident organisms to chronic contamination and frequently serve

as sentinel systems for monitoring environmental health (Selin, 2009; Maznikova et al., 2024). Much of what is known about mercury's toxicity comes from controlled laboratory studies, which have established dose-dependent impairment of reproduction, behaviour, and survival (Heinz, 1979; Wolfe et al., 1998). Mercury is therefore an important pollutant not only because of its ubiquity, but because it is known to cause substantial harm, yet translating these laboratory-measured effects to wild populations requires knowledge about realised exposure levels, which can vary considerably among individuals and environments (Evers, 2018).

The sources of variation in exposure to mercury in wild organisms are numerous and can combine additively or counteract one another. Consequently, despite the ubiquitous presence of mercury in the environment, there can be extensive disparities in its concentrations in wild organisms, both within and among species. These differences arise from a range of extrinsic sources, including habitat type, proximity to industrial or agricultural sites, and exposure time (Evers et al., 2005; Dauwe et al., 2004) and intrinsic sources, including accumulation rates and physiological detoxification processes (Basu et al., 2014). Human activities such as industry, agriculture, and mining are known to elevate local mercury levels, but natural factors also contribute to spatial heterogeneity in environmental mercury (Wang et al., 2019). Aquatic habitats are often hotspots for mercury exposure because contaminated sediments and flowing waters facilitate the transport of mercury, and microbial processes in sediments convert it into methylmercury (Selin, 2009; Hsu-Kim et al., 2013). In particular, anaerobic conditions in sediments favour sulphate-reducing bacteria, which are the primary methylators of inorganic mercury, leading to its accumulation over time (Compeau & Bartha, 1985). In contrast, mercury in terrestrial environments is mostly shaped by soil properties and atmospheric deposition; although soils can accumulate substantial mercury over time, including in remote areas via long-range transport, aerobic conditions generally limit methylation, resulting in lower bioavailability to terrestrial food webs compared to aquatic systems (Driscoll et al., 2013; Kalisinska, 2019). Landscape configuration, including the degree of urbanisation, forest cover, and agricultural intensity, can therefore influence both the delivery of mercury to ecosystems and its subsequent bioavailability to consumers.

Because mercury bioaccumulates over time, older individuals and longer-lived species typically show higher mercury concentrations, and dietary differences further shape how much mercury individuals accumulate (Bertram et al., 2024a). Birds are particularly informative as bioindicators of mercury contamination because they display diverse foraging strategies, habitat use, and migratory behaviours (Maznikova et al., 2024; Vizuete et al., 2019). Additional sources of inter-individual and interspecific variation include heritable traits (Buck et al., 2016), moulting patterns (Carravieri et al., 2014), and excretion (Monteiro & Furness, 2001), as well as, in females, the transfer of mercury into eggs, likely modulated by egg size, composition, and clutch size (Ackerman et al., 2020). Moulting and egg-laying can both function as detoxification routes in birds: mercury deposited into growing feathers is effectively sequestered once the feather is fully grown and metabolically inert (Bottini et al., 2021), while mercury transferred into eggs is eliminated from the female's organism, potentially at a cost to embryo growth (Hallinger & Cristol, 2011). In addition, individual foraging behaviour also shapes patterns of mercury accumulation. Juveniles, for example, often forage on different prey than adults (Yoerg, 1998; Davies et al., 2022). Consequently, even individuals occupying similar environments may differ markedly in mercury concentrations due to physiological, behavioural, and life-history traits and even individuals with similar mercury concentrations may experience different degrees of harm, depending on individual sensitivity to mercury toxicity (Basu et al., 2014). Understanding inter-individual variation in mercury concentration is crucial, as elevated mercury has been associated with adverse health effects, impaired reproduction, and decreased survival (Evers, 2018; Kalisinska, 2019). Identifying the sources of exposure and individual-level variation can support more effective monitoring and conservation strategies (Seewagen, 2010).

In this paper we investigate the sources of variation in exposure to mercury in a natural population of white-throated dippers (*Cinclus cinclus*) inhabiting rivers spanning gradients of legacy industrialisation, urbanisation, agriculture, and elevation in the Chartreuse mountains, France. By repeatedly sampling individuals, territories, and rivers, we partitioned

variance in mercury concentrations among environmental (e.g. urbanisation, land cover, altitude, human footprint), spatial (territory, river), temporal (year), and individual identity. Specifically, we (1) quantified the mercury concentration in 777 feather samples from 451 adult females, which allowed us (2) to estimate repeatability in mercury exposure at individual, territory, river, and year levels, and (3) to test to what extent landscape features (human footprint index, forest cover, altitude) contribute to spatial variation in mercury exposure. By partitioning mercury concentration variance across individual and spatial scales, we aimed to identify possible territories or rivers with persistently elevated relative mercury exposure, which persist independently of population turnover and are therefore critical targets for long-term monitoring and mitigation efforts in riverine ecosystems. Further, while identifying consistently high-exposed individuals may not alone reveal the traits (e.g. age, sex, foraging specialisation) underlying elevated risk, it is an important first step before such variation can inform individual-level risk assessment or mitigation.

Materials and methods

Study species

The white-throated dipper, also known as the European dipper (hereafter “dipper”), is a small passerine widely distributed along rivers and lakeshores throughout Europe and parts of the Palearctic. Dippers are highly adapted to running aquatic systems, where they forage primarily on aquatic invertebrates by diving or walking along riverbeds. During the pre-breeding period, females may adopt a more piscivorous diet (Morrissey et al., 2010). This species lives along a range of riparian habitat types, including urban, agricultural, and forested rivers, and typically constructs nests above or very close to the water, utilising both natural and artificial structures. Dippers are a resident species and show both short natal dispersal (~ 5 km in males, ~ 11 km in females in our study population; B. Doligez, unpublished data) and near-absent breeding dispersal, such that individuals typically remain on the same stretch of river throughout their lives once settled. This sedentary lifestyle, combined with their high trophic position in riverine food webs, makes dippers well suited as biomonitors of environmental mercury and other pollutants in riparian environments (Maznikova et al., 2024; Pedersen et al., 2020; Silverthorn et al., 2018).

Study site

Field data were collected in the Chartreuse mountains region in south-eastern France (centroid of the study area: 45.41377° N, 5.73831° E), where a natural dipper population is monitored along 11 rivers spanning a gradient of urbanisation degree and altitude (185–1111 m above sea level). Both natural nesting sites (N = 332) and artificial nest boxes (N = 385) are monitored systematically every year. From 2014 to 2025, a total of 9,790 dippers were ringed (N = 7,870 as nestlings and 1,920 as adults) at 730 unique territories (Fig. 1). Each year, around 400 to 450 adult dippers were captured using mist nets from January to June, with biometric information recorded at every capture. Undertail covert feathers were collected for mercury analysis, stored in plastic bags at room temperature, and protected from light until laboratory processing. Individual identification and breeding territory assignment were based on unique ring numbers and colour band combinations, combined with video recordings and field observations at active nests.

Sampling strategy

Given the large number of captured and sampled adults, a subset was selected for mercury analysis. First, only females were selected for analysis to avoid potential confounding effects associated with sex-related differences in mercury bioaccumulation. Thus, sex differences were not explored here. Second, among females, only individuals aged two years or more were selected to ensure that feather mercury concentration reflected contamination from their established breeding territory. Indeed, feathers are grown during the post-breeding moult (late summer) and most dippers show very high breeding territory philopatry after settling at one year of age; individuals aged two years or more captured in a given year have therefore moulted on their established territory the preceding summer and this design thus allows reliable

assignment of feather mercury levels to a specific territory. Repeated sampling of different individuals on the same territories and individuals occupying multiple territories across years (usually close to one another) were purposefully prioritised for inclusion to further disentangle intrinsic (individual) versus extrinsic (territory) sources of mercury variation. Because dippers otherwise show very strong territory fidelity after settlement, individuals occupying multiple territories across years are less common in the population as a whole; our dataset therefore deliberately oversamples these individuals relative to their natural frequency, and the proportion of multiple-territory individuals reported below should be interpreted as a feature of this targeted sampling subset rather than as representative of dispersal rates in the wider population. Our final selected dataset comprised 451 ringed adult females, with an average of 1.72 feather mercury measurements per individual (median = 1, range 1–3), and 43% of individuals (193/451) contributing repeated measurements (≥ 2 samples). At the territory level, we had mercury measurements from 255 territories. Of these, 124 territories were associated with a single sampled individual, 71 with two different individuals, and 60 with three or more individuals for the selected samples over the study period. Most individuals were recorded in only one territory (413/451), but 38 individuals (8%) were sampled in more than one territory, typically two territories and at most three. In sum, we analysed 777 feathers from 451 individuals sampled in 11 rivers (Fig. 1) and over 9 years (2017 to 2025).

Feather preparation and mercury analysis

Total mercury was measured in undertail covert feathers, used as a proxy for methylmercury exposure since methylmercury typically represents more than 90% of mercury detected in avian feathers (Renedo et al., 2017). To minimise external contamination, feathers were rinsed with deionised water, submerged in a 2% alkaline solution (RBS-50; Sigma-Aldrich, St. Louis, MO, USA), and ultra-sonicated for 5 minutes, following feather-cleaning protocols established in other avian mercury studies (Keute et al., 2024; Bertram et al., 2022). Feathers were then rinsed again with deionised water, oven-dried at 65°C overnight (at least 12 hours), and weighed to the nearest 0.1 mg (dry weight).

For mercury quantification, entire feathers were placed in nickel boats and thermally decomposed at 950°C for 4 minutes using a Direct Mercury Analyser (DMA-80 evo, Milestone Srl, Sorisole, Italy). Mercury released during decomposition was trapped on a gold amalgamator and measured via atomic absorption spectrometry at 253.7 nm following standardised protocols (U.S. Environmental Protection Agency, 2007). Quality control measures included blanks and certified reference materials (CRM) were measured every ten samples and at the start/end of each batch. Feathers measured in 2021 were validated with bovine liver (NIST 1577c; recovery: $102.2 \pm 1.8\%$, $n = 37$), feathers measured in 2024 were validated with lobster hepatopancreas (TORT-3; recovery: $98.4 \pm 5.5\%$, $n = 42$), and feathers measured in 2025 were validated with human hair (ERM-DB001; recovery: $92.7 \pm 3.9\%$, $n = 20$). The detection limit for feather samples was 0.011 ng, and all samples were above this threshold. Feather mercury concentrations are reported in $\text{mg}\cdot\text{kg}^{-1}$ dry weight.

For a subset of birds, two undertail covert feathers were measured to assess biological repeatability. These feathers were collected on the same day ($N = 242$ feathers from 121 individuals). Repeatability was very high ($R = 0.94$, 95% CI = 0.91–0.95), indicating negligible within-individual variation in mercury from samples collected in the same day from the same body area. Because biological repeatability was so high, a single feather measurement per individual was prioritised when building the main dataset, averaging duplicate feathers where available in order to maximise sample size and statistical power. Previous analyses in this population have also shown that feather mercury is positively correlated with blood mercury, supporting the use of feather mercury as a reliable proxy of mercury exposure in dippers (Hinninger et al., in prep).

Statistical analyses

All statistical analyses were performed in R v4.5.3 (R Core Team, 2026). Feather mercury concentrations were log-transformed to meet assumptions of normality prior to analysis. For linear mixed models, all continuous predictors

were scaled (mean = 0, SD = 1) prior to analysis to facilitate model fit and interpretation. Statistical significance was defined as estimates with 95% confidence intervals not overlapping zero or p-values ≤ 0.05 .

Repeatability and variance partitioning

Repeatability of log-transformed feather mercury concentrations was estimated using the *rpt* function from the *rptR* package (Stoffel et al., 2017), assuming a Gaussian error distribution. Single-factor models were first fitted to obtain marginal repeatability estimates for each grouping factor (individual, territory, river, and year) separately. A comprehensive four-factor model (individual + territory + river + year) was used to partition variance across hierarchical levels. Two- and three-factor models were also fitted to explore how variance is shared between hierarchical spatial levels before fitting the comprehensive four-factor model, and Akaike Information Criteria (AIC) were compared across this full set of nested models (Supplementary Table S1). Each model was evaluated using 100 parametric bootstraps and 100 iterations, with empirical 95% confidence intervals used to determine whether repeatability differed from zero. AIC values of the underlying mixed models were compared to assess alternative random-effects structures (Supplementary Table S1).

Human footprint index at the territory level

To characterise landscape structure around territories and reduce collinearity among land-use variables, we conducted a principal component analysis (PCA) on four z-standardized predictors: (i) percentage of land cover classified as urban, (ii) percentage of land cover classified as agricultural, and (iii) total building surface, each quantified within an elongated buffer following the river channel (500 m along the watercourse by 250 m from the bank, centred on the nest), and (iv) number of inhabitants in the municipality. Road density and road length were also screened as candidate variables but dropped before the PCA: road length was near-perfectly correlated with road density, and road density was in turn near-perfectly correlated with urban land cover, so retaining either would have reintroduced the same collinearity the PCA is meant to remove. These variables were chosen as proxies for distinct pathways of anthropogenic mercury input: urban land cover and building surface reflect impervious surface extent and associated atmospheric mercury deposition and surface-runoff mobilisation (Eckley & Branfireun, 2008); agricultural land cover (mainly cattle pasture in this catchment) reflects grazing-related soil disturbance and nutrient loading, which can mobilise sediment and promote methylmercury production (Gygax et al., 2019); and number of inhabitants reflects broader demographic pressure, consistent with its role as a core component of established human footprint indices (Venter et al., 2016a, b). Unlike the other three variables, inhabitant counts were available only at the municipality level rather than as a spatially continuous 250 m metric; we retained this variable for its conceptual relevance to human footprint, while acknowledging this coarser spatial resolution. The first principal component (PC1) explained 64.0% of the total variance and represented a gradient from low human impact territories to more urbanised territories, with higher scores associated with larger building surface and higher local urbanisation. The second component (PC2) explained a further 18.0% of the variance, driven primarily by agricultural land cover; number of inhabitants loaded moderately on PC1 (0.730) and only weakly on PC2 (-0.042), with its strongest loading occurring on the lower-order PC3 (-0.682; Supplementary Table S4), consistent with its coarser spatial resolution relative to the other variables. We defined PC1 as a composite 'human footprint index' at a 250 m scale around each territory ($HFI_{\text{territory}}$) and used this score as the only PCA-derived predictor in linear mixed-effects models of log-transformed feather mercury concentrations (see Supplementary Tables S2–S4 and Supplementary Fig. S2 for PCA details). Our $HFI_{\text{territory}}$ values were moderately correlated with the Global Human Footprint Index calculated by the Wildlife Conservation Society (Venter et al. 2016a; b) at 1 km resolution around each territory (Pearson's product-moment correlation, $r = 0.481$, 95% CI: 0.448–0.513), indicating that our fine-scale, territory-level index captures a similar underlying gradient of human pressure as this established global measure.

Mixed-effects model of mercury exposure

Sources of variation in mercury exposure were analysed using linear mixed-effects models fitted with the *lmer* function in the *lme4* package (Bates et al., 2015). Because the PCA-derived human footprint index required complete data on number of inhabitants and building surface, 32 of the 777 feather measures lacking one or more of these variables were excluded from this model, yielding a final sample size of 745 measures from 433 individuals. The response variable was log-transformed feather mercury concentrations, and the model included as fixed explanatory variables the altitude of the territory, our measure of human footprint index of the territory ($HFI_{\text{territory}}$), and the percent land cover within 250 m of the territory defined as forest (For details on variables see Supplementary Table S2). Percent land cover defined as forest was excluded from the PCA and tested as a separate predictor instead to reflect canopy-driven atmospheric mercury retention rather than anthropogenic pressure (Driscoll et al., 2013; Luo et al., 2025). As urban, agricultural, and forest cover are compositional (summing to 100%), including all three covariates individually without using the PCA approach caused severe multicollinearity (variance inflation factors 16.97–22.49; Supplementary Table S5). Furthermore, because several landscape covariates may be partially confounded with river identity (e.g., altitude varies systematically among rivers), retaining river and territory as random effects risked absorbing variance we sought to attribute to these fixed effects, masking their true influence. We therefore fitted this model with a simplified random-effects structure, retaining only individual identity and year as random intercepts. For comparison, we nevertheless also fitted a model with the same fixed effects with the full hierarchical random-effects structure (individual, territory nested within river, river, and year; Supplementary Table S6). We also fitted a model replacing $HFI_{\text{territory}}$ with the raw percentage of urban land cover within 250 m of the territory, to confirm that the human footprint effect was not an artefact of the PCA construction (Supplementary Table S7). We additionally fitted a model including the second principal component (PC2) from the landscape PCA alongside PC1 (Supplementary Table S8). Model estimates, standard errors, Wald 95% confidence intervals, and p-values for fixed effects were extracted, and partial effect plots were generated using the *effects* package (Fox & Weisberg, 2019). Normality and homoscedasticity of model residuals were verified by visual inspection using the DHARMA package in R (Hartig, 2024). Collinearity among fixed effects was low to modest ($|r| \leq 0.30$, all variance inflation factors ≤ 1.15 ; Supplementary Fig. S3 and Table S9).

Spatial autocorrelation diagnostics

To assess whether unexplained spatial structure remained after accounting for features of the local environment, residual spatial autocorrelation was evaluated for the main model detailed above. Residuals were averaged at the territory level, and Moran's I was calculated using k-nearest-neighbour ($k = 4$) spatial weights based on territory coordinates with the *sp* package (Pebesma & Bivand, 2005) and *spdep* package (Bivand et al., 2013; Bivand & Wong, 2018). We chose this method rather than a fixed-distance threshold, since territory length varied substantially among rivers and unoccupied unfavourable habitats occasionally occur along rivers (e.g. stagnant dam water reservoirs). To confirm that our results were not sensitive to the choice of $k = 4$ neighbouring territories, we repeated the analysis using $k = 3, 5$, and 6 nearest neighbours; Moran's I remained non-significant across all values of k tested ($I = 0.023$ to 0.045 , all $p \geq 0.15$; Supplementary Table S10), confirming that our conclusions were robust to the choice of k . The Moran's I statistic, its expected value under spatial randomness, and the associated p-value were used to assess the extent to which the mixed effect model captured spatial clustering in mercury exposure.

Results

Feather mercury concentrations in adult female dippers aged two years or more were highly right-skewed, with most individuals showing low to moderate concentrations and a long tail of higher concentrations. Across 777 measures ($N = 451$ unique individuals), mean $\pm$ SD total mercury concentration was $1.62 \pm 0.95 \text{ mg} \cdot \text{kg}^{-1}$ dry weight, ranging from 0.27 to $7.54 \text{ mg} \cdot \text{kg}^{-1}$ dry weight (see Supplementary Fig. S1 for data spread). Overall, 6 measures (i.e., 0.8%) corresponding to four individuals in the sample population had mercury concentrations above $5 \text{ mg} \cdot \text{kg}^{-1}$ dry weight, considered as the approximate toxicity thresholds for measures in avian feathers (Burger and Gochfeld, 1997).

Repeatability of feather mercury concentrations

Repeatability analyses where each random factor was modelled separately showed very strong repeatability of feather mercury concentrations at the individual level ($R = 0.80$), lower but moderate repeatability estimates at the territory ($R = 0.53$) and river ($R = 0.31$) levels, and low estimate for year ($R = 0.08$) (Table 1). When all four random effects were modelled jointly, results revealed that the strong repeatability at the individual level is (re)distributed between individual ($R = 0.42$), river ($R = 0.26$), and territory ($R = 0.12$) (Table 1; $0.42 + 0.12 + 0.26 = 0.80$). This four-factor random model had the lowest AIC among all candidate random-effects structures (Supplementary Table S1). Across all models, the 95% confidence intervals for each random-effect variance component excluded zero, indicating that all grouping factors contributed significantly to among-individual variation in feather mercury concentrations regardless of the random-effects structure.

Table 1

Repeatability (R and 95% confidence intervals) of log-transformed feather mercury concentrations from single-factor and multi-factor models at the individual, territory, river, and year levels, with Akaike's Information Criterion (AIC) for the corresponding mixed-effects models used to compare alternative random-effects structures. The best model (based on AIC) is highlighted in bold.

Model	Individual	Territory	River	Year	AIC
N = 777 observations	N = 451	N = 255	N = 11	N = 9	
Individual only	0.80 [0.76, 0.84]				912.4
Territory only		0.53 [0.47, 0.60]			1050.2
River only			0.31 [0.12, 0.46]		1033.9
Year only				0.08 [0.02, 0.21]	1218.1
Individual + Territory + River + Year	0.42 [0.31, 0.55]	0.12 [0.06, 0.20]	0.26 [0.06, 0.43]	0.04 [0.00, 0.08]	730.0

Effects of landscape features on feather mercury concentrations

We found significant effects of both altitude and $HFI_{\text{territory}}$ on log transformed feather mercury concentrations (Table 2). Feather mercury concentrations were higher at lower altitudes, and contrary to our expectation, were also higher in territories with lower $HFI_{\text{territory}}$, and thus supposedly less exposed to current human presence and activity (Fig. 2). Forest land cover was not related to feather mercury concentrations (Table 2).

Table 2

Linear mixed effects model of log transformed feather mercury concentrations in adult female dippers in the Chartreuse mountains (N = 433 individuals, n = 745 measures). Fixed effects include forest land cover, altitude, and the human footprint index of the territory ($HFI_{\text{territory}}$, see text for calculation); random intercepts for individual identification and year account for hierarchical and repeated measures structure.

Marginal and conditional R^2 values are reported.

Fixed effects	Estimate	95% CI	p value
Intercept	0.304	[0.217, 0.392]	< 0.001
Forest land cover (%)	0.015	[- 0.032, 0.062]	0.528
Altitude (m)	-0.168	[- 0.216, -0.120]	< 0.001
$HFI_{\text{territory}}$	-0.119	[- 0.161, - 0.076]	< 0.001
Random effects	Variance		
Individual	0.196		
Year	0.012		
Residual	0.052		
R^2_c / R^2_m	0.822 / 0.114		

Spatial autocorrelation

Residual diagnostics for the linear mixed model showed no statistically significant residual spatial autocorrelation at the territory scale. Moran's I calculated on territory-averaged residuals with k-nearest-neighbour ($k = 4$) spatial weights suggesting no remaining residual spatial structure (Moran's I = 0.033, expected I = - 0.004, $p = 0.38$; Supplementary Table S10, Supplementary Fig. S4). The sensitivity analysis across $k = 3$ to 6 nearest neighbours confirmed that this result was robust, with Moran's I remaining non-significant across all values of k tested (I = 0.023 to 0.045, all $p \geq 0.15$; Supplementary Table S10).

Discussion

To explore the sources of variation in mercury exposure in the wild and disentangle environmental from individual effects, we used repeated measures of mercury concentrations in feathers of dippers from a natural mountainous population. Overall, feather mercury concentrations showed substantial variability among individuals, territories and rivers, but quite low variation between years in contrast, reflecting combined effects of individual and local environmental processes (Kalisinska, 2019; Evers et al., 2005; Dauwe et al., 2004; Basu et al., 2014; Eagles-Smith et al., 2018). Mean mercury levels ($1.62 \pm 0.95 \text{ mg} \cdot \text{kg}^{-1}$ dry weight) were similar to those reported for dippers and other aquatic birds inhabiting moderately contaminated freshwater and estuarine habitats (Pedersen et al., 2020; Lucia et al., 2010), with nonetheless 0.8% of measures (0.9% of the individuals) in the sample population exceeding the $5 \text{ mg} \cdot \text{kg}^{-1}$ toxicity threshold proposed for measures in avian feathers (Burger and Gochfeld, 1997). This combination of a moderate population mean with a small fraction of high value individuals is consistent with a system influenced by both spatially concentrated (point-source) and more diffusely distributed contamination, where most individuals are likely to experience background exposure while a small subset appears to accumulate burdens approaching levels of toxicological concern (Evers et al., 2005; Jackson et al., 2020).

Repeatability estimates showed that individual identity explained the largest proportion of variance in mercury concentrations, suggesting relatively consistent exposure patterns that may be tied to behavioural or intrinsic traits such as foraging choices, microhabitat use or detoxification efficiency (Jackson et al., 2020; Bertram et al., 2024b; Basu et al., 2014). White-throated dippers exhibit strong territory fidelity once settled, i.e. very restricted breeding dispersal (B. Doligez, unpublished data); combined with the traits mentioned above, this fidelity is likely to contribute to persistent exposure signatures over multiple years, as individuals likely repeatedly exploit a limited set of micro-habitats and prey resources, although direct evidence for this is lacking. Accordingly, the very high repeatability (80%) at the individual level in the single-factor model was reduced by half (42%) when river and territory were included as additional random factors in the full model, suggesting that part of this apparent individual-level consistency is confounded with stable spatial differences among territories, consistent with the strong territory fidelity of dippers. This interpretation is further supported by the low importance of sampling year in accounting for feather mercury concentrations (4% in the four-factor model), indicating that year-specific environmental conditions contribute comparatively little to mercury exposure relative to the more persistent spatial and individual sources of variation identified above. This temporal stability reinforces the idea that variation in exposure is mainly driven by persistent spatial and individual characteristics. Because individual repeatability estimates can provide an upper limit for heritability estimates (Wilson, 2018), it would be interesting to quantify the contribution of genetic differences among individuals to variation in feather mercury concentrations. This is particularly relevant for understanding the capacity of natural populations to adapt to anthropogenic stressors such as pollution (Whitehead et al., 2017; Loria et al., 2019). In the common tern (*Sterna hirundo*), feather mercury repeatability and heritability have been estimated at 64% and 9%, respectively (Bertram et al., 2024b), yet the genetic and physiological pathways underlying individual variation, including mercury uptake, storage, and excretion, remain poorly understood.

River and territory explained a moderate amount of variation in feather mercury concentrations in single factor models (respectively 31% and 53% for river and territory), with this variance being reduced (to 26% for river and 12% for territory) in the full model. Once individual and year effects were accounted for, the moderate consistency of mercury measurements within rivers, and to a lesser extent within territories, suggests relatively spatially stable contamination that may persist regardless of which individual occupies a given territory. Because river-level consistency exceeded territory-level consistency in the full model, this pattern points to probable long-term sources of mercury operating at least partly at a spatial scale broader than individual territories (Howie et al., 2018; Evers et al., 2005). This could be due to small-scale environmental differences, from the territory to river level, in water chemistry, sediment composition, prey community structure, hydromorphology, and local methylation dynamics that can alter mercury bioavailability in aquatic invertebrates and biomagnification along the food chain (Paranjape & Hall, 2017; Ullrich et al., 2001). Because dippers show strong territory fidelity across years, however, it remains difficult to fully separate intrinsic individual differences from persistent extrinsic differences among territories. This issue mirrors broader ecological debates about the relative importance of individual specialisation versus spatial heterogeneity in shaping contaminant burdens (Bolnick et al., 2003; Araújo et al., 2011; Baak et al., 2024; Brand et al., 2025). Experimental work using translocations of individuals across territories and rivers or experimental manipulations of diet could help disentangle these processes.

To gain additional insight into whether measurable landscape variables could account for this small-scale spatial variation, we examined the influence of landscape features known to potentially account for variation in mercury contamination. Contrary to our initial prediction, our index of human footprint around each territory ($HFI_{\text{territory}}$), reflecting present day landscape urbanisation, was found to negatively relate to mercury concentration. This suggests that dippers living on territories characterised by higher urbanisation levels in the surrounding area had lower mercury concentrations than on territories with lower urbanisation levels. In riverine ecosystems, mercury contamination can also be driven by landscapes dominated by forests acting as sinks for atmospheric mercury (Luo et al., 2025), which is deposited via litterfall undergoing *in situ* methylation on the forest floor or in river sediments. Because both forest cover and aerial currents can vary with topography in mountainous landscapes, altitude could also relate to mercury concentration

(Zhang et al., 2013; Townsend et al., 2014). Here, forest cover showed no relationship with mercury concentration. Altitude, however, was significantly negatively associated with mercury concentration. In our case, legacy contamination associated with historical mining and industry, likely concentrated in low-altitude, non-urban areas away from town centres, may have decoupled present-day land use from current exposure patterns. This could explain why contemporary urban or forest cover does not reliably reflect the location or intensity of past emissions, and why mercury concentrations were higher at lower altitudes. Although urbanisation typically coincides with elevated metal and metalloid concentrations (Bradl, 2005), similar patterns of reduced metals in urbanised systems have been previously reported in birds (Chatelain et al., 2021). This negative relationship may reflect lower methylation in urban rivers, driven by differences in sediment redox conditions and sulfate/sulfide chemistry that reduce Hg(II) availability for methylation (Marvin-DiPasquale et al., 2009; Ullrich et al., 2001). Overall, the mercury contamination observed in this study area is consistent with a primary contribution from legacy pollution rather than ongoing industrial discharge, as historical land use included mercury-relevant industries (i.e., silk and textile processing, paper mills, and tanneries); although industrial activity itself remains substantial along rivers such as the Fure and Morge, regulations now restrict the use and thus release of mercury, such that current inputs from these industries are likely close to negligible, barring accidental releases (Syndicat Intercommunal du Bassin de la Fure, 2011). Historical research on past industrial land-use is still needed to identify the potential sources of legacy pollution and the nature of pollutants in this area.

Although this study provides a detailed picture of individual and spatial variation in mercury exposure, at least three limitations should be acknowledged. First, feather mercury concentrations integrate exposure over the moult period only, and combining feather, blood, and egg measurements would better capture temporal dynamics including maternal transfer to eggs. Yet, previous research in birds shows that mercury levels correlate between blood and feathers (Bottini et al., 2021; Bertram et al., 2026) and between parental blood and egg mercury (Bertram et al., 2025), including whole blood and feathers in our population of dippers (Hinninger et al., in prep). This supports the use of feathers as a low-invasive method to monitor mercury contamination to gain knowledge on individual and local environmental processes shaping mercury exposure. Second, we focused exclusively on females aged two years or more, so patterns of exposure and variance partitioning may differ in males or younger age classes that may use alternative habitats or prey and may have different physiological detoxification capacities. Whether this sampling strategy also incurs a bias due to the choice of birds surviving at least two years is unknown. Our inferences therefore apply primarily to old adult female dippers, and future work should explicitly test whether the same spatial and individual patterns hold in other demographic classes. Because both sexes show high territory fidelity over the years once settled, which results in correlated exposure to mercury contaminations within breeding pairs (Hinninger et al., in prep), we would expect similar findings in males aged two years or more. Finally, and most importantly, all inferences about environmental drivers are indirect, because we did not measure mercury concentrations or methylation rates in water, sediment, or prey. Direct quantification of mercury and related geochemical parameters in the environment, coupled with sampling of females, males and juveniles, would allow drawing stronger inferences about the mechanisms proposed here and could help identify the specific biophysical contexts that generate exposure hotspots.

Conclusions

This study shows that mercury exposure in dippers of the Chartreuse mountains is shaped jointly by persistent, territory-level contamination and stable individual differences, with the species' strong territory fidelity once settled likely reinforcing both signals with age. Repeated sampling of marked individuals revealed very low year-to-year variation relative to variation among individuals, territories, and rivers, indicating that exposure patterns are set by long-standing spatial and individual factors rather than short-term fluctuations. Present-day landscape features, and in particular our territory-level human footprint index, were strong predictors of this spatial pattern, but in the direction opposite to what current human activity alone would predict, most plausibly because they capture legacy contamination from historical rather than ongoing sources.

These results demonstrate the value of combining repeatability analyses with mixed-effects models on repeated samples of marked individuals: this approach can reveal persistent spatial and individual signatures that a single cross-sectional survey would miss. This adds to a growing body of work showing that individual identity itself carries meaningful, replicable information about contaminant exposure. Our findings support prioritising long-term, individual-based monitoring of contaminated riverine systems alongside landscape-level predictors and point to genetic and physiological sources of individual variation as a promising direction for future work.

Declarations

All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

M.O., B.D. and P.B. conceived and designed the study, with additional input from G.N. Funding was acquired by B.D. and P.B. for the study. M.O. and B.D. curated the data. M.O. led the laboratory investigation, with support from L.H. in the laboratory. M.O., B.D. and P.B. developed the methodology, with support from G.N. For the formal analysis, M.O. led, with P.B. and B.D. supporting. P.B. and B.D. led supervision of the project, with G.N. supporting. M.O. prepared the visualizations and led the writing of the original draft. All authors validated the results, and all authors reviewed and edited the manuscript.

Ethics approval

All procedures were conducted under permits from the C.R.B.P.O. (Personal Ringing Programme n° 655), DREAL (Isère and Savoie; authorisations 38-2018-0601015, 2018-727, 38-2023-0807-00007, 74-2023-09-22-00007) and approved by the University of Lyon 1 ethical committee (APAFIS287292020121716192778 v4).

Data and resource availability

All data supporting the findings of this study are available within the article and its supplementary information. Additional materials, including the underlying databases and R scripts used for analysis, are archived in the Vogelwarte Open Repository and Archive and will be assigned a DOI upon acceptance. For the purposes of peer review, these materials are currently provided as supplementary files.

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Figures

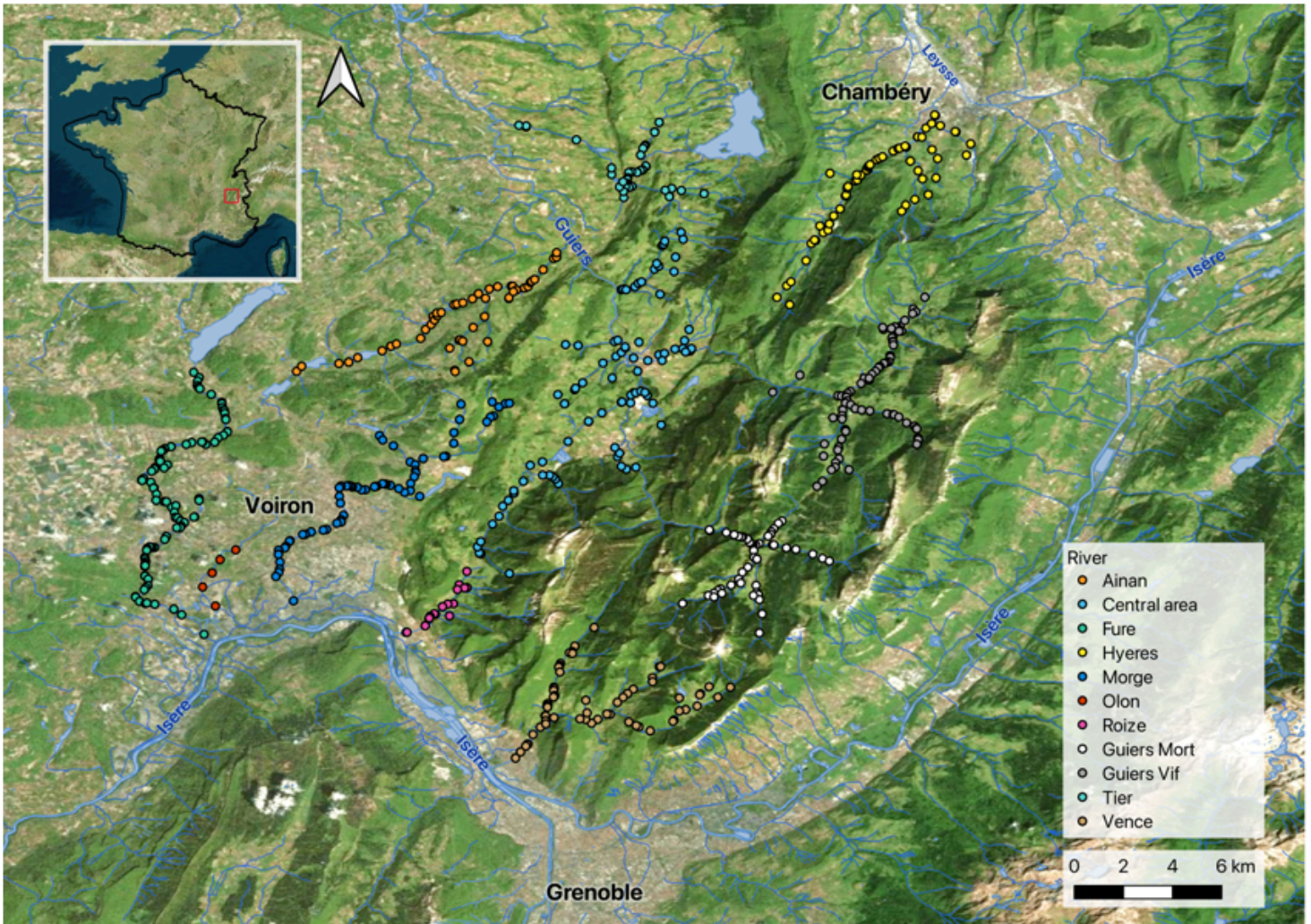


Figure 1

Map of white-throated dipper territory locations in the Chartreuse mountains, southeastern France. Circles show individual territories, coloured by river identity as indicated by the legend; note that the central area is composed of several smaller tributaries feeding into the main central river, the Guiers. Terrain shading and selected cities provide topographic and geographic context, and the scale bar and north arrow indicate distance and orientation. The full map of France is shown in the inset (top left), with the black rectangle indicating the study area. Map created using the free and open-source software QGIS©. Map data © OpenStreetMap contributors

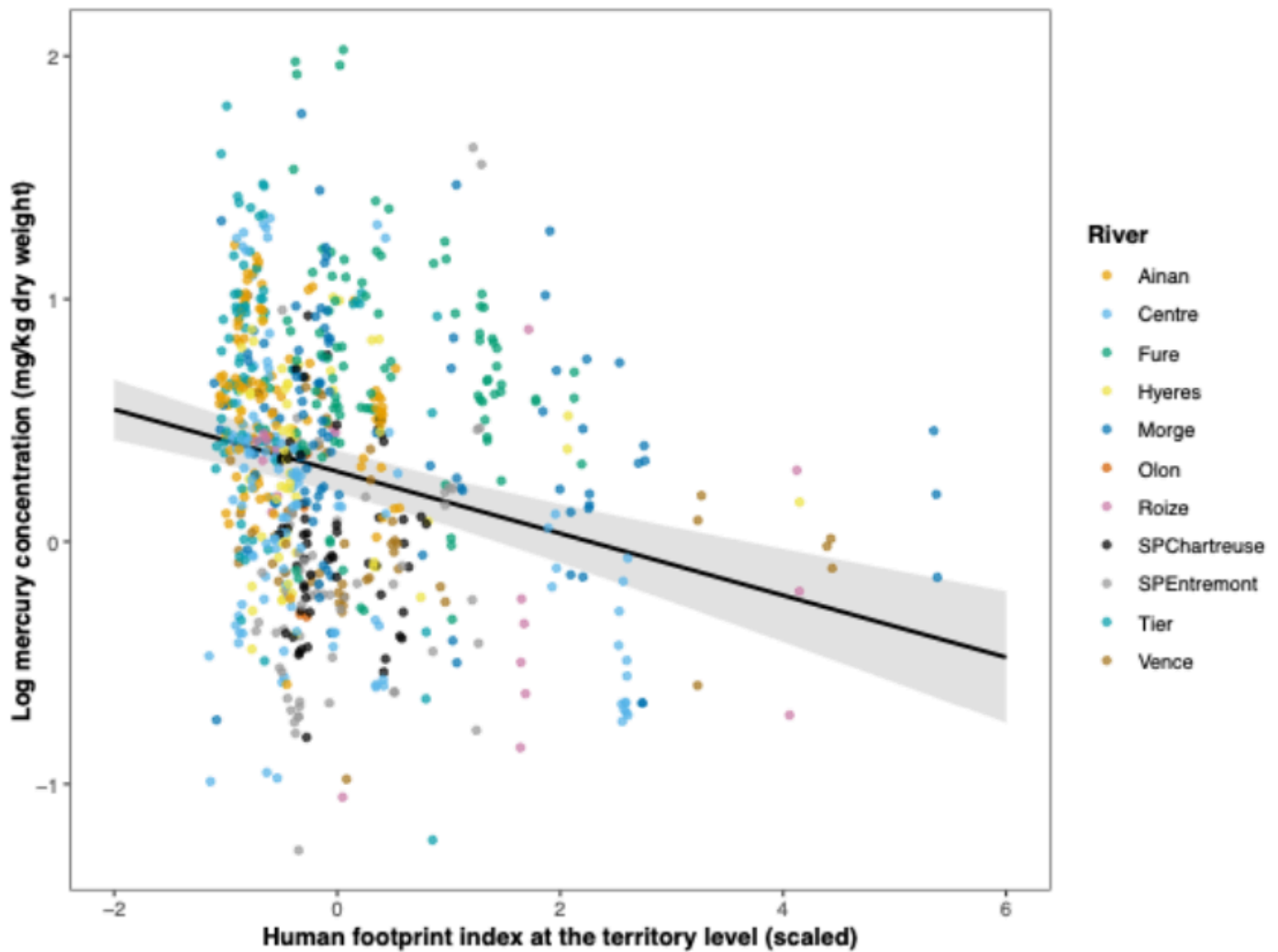


Figure 2

Relationship between the human footprint index of the territory (PC1, see text; scaled) and log-transformed mercury concentration in dippers (N = 433 individuals, n = 745 measures). Points show individual feather mercury concentration values coloured by river (see Fig. 1); the solid line and shaded area represent predicted mean and 95% confidence interval from a linear mixed-effects model including forest cover, human footprint index, and altitude as fixed effects, and individual and year as random effects

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