Environmental Research 307 (2026) 125508

Contents lists available at ScienceDirect

Environmental Research

journal homepage: www.elsevier.com/locate/envres

Embryonic exposure to mercury contamination is associated with elevated corticosterone and lower body condition in wild Smooth-fronted caiman hatchlings

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ARTICLE INFO

Keywords:
Claws
Crocodylians
Contaminant
Endocrine disruption
Maternal transfer

ABSTRACT

Mercury (Hg) is a worldwide contaminant that affects all ecosystems, yet most evidence of its biological impacts comes from fish, birds, and mammals, leaving reptiles comparatively understudied. Crocodylians may be particularly vulnerable to Hg due to their long lifespans, high trophic positions, and occurrence in tropical and subtropical regions affected by artisanal and small-scale gold mining. We investigated the effect of Hg contamination during embryonic development in the Smooth-fronted caiman (*Paleosuchus trigonatus*, n = 15), using claws, scutes and red blood cells (RBCs)as a non-invasive proxy for in-ovo exposure. We found a positive relationship between plasma corticosterone (CORT) concentration and claw ($R^2 = 0.65$, $p < 0.001$), scute ($R^2 = 0.67$, $p < 0.001$) and RBCs ($R^2 = 0.39$, $p = 0.018$) Hg concentrations, suggesting that even low embryonic Hg exposures may alter the endocrine status of hatchlings. We further assessed body condition in relation to CORT concentration to explore potential phenotypic effects and found a negative relationship ($R^2 = 0.48$, $p = 0.004$). Our findings support the use of keratinized tissues as a minimally invasive biomonitoring matrix for assessing in-ovo Hg exposure in crocodylians and also highlight the need to integrate contaminant dynamics into conservation strategies for species inhabiting Hg-impacted ecosystems.

1. Introduction

Environmental contamination is one of the main drivers of biodiversity loss (Jaureguiberry et al., 2022), where mercury (Hg) is among the most concerning contaminants due to its widespread distribution, persistence, and toxicity to humans and wildlife (Driscoll et al., 2013; Eagles-Smith et al., 2018). Despite Hg being naturally present in the environment, with sometimes high background levels such as in the neotropics, Hg release is mainly increased by artisanal and small-scale gold mining (ASGM) and fossil fuel combustion, generating hotspots of exposure for wildlife in aquatic habitats (GMA, 2019; Qiu et al., 2025).

Once released into aquatic ecosystems, microorganisms transform Hg into methylmercury (MeHg), the most bioavailable and toxic form, which biomagnifies through the trophic chain and accumulates in predators (Benoit et al., 2003; Podar et al., 2015). In vertebrates, MeHg has been linked to immunotoxicity (Zhang et al., 2016; Crowe et al., 2017), neurobehavioral impairment (Bridges et al., 2016; Landler et al., 2017), and disruption of reproductive processes, with consequences for offspring quality and survival (Hopkins et al., 2013; Tartu et al., 2013; Lemaire et al., 2021a). While the impact of MeHg has been well studied in mammals, fish, and birds, reptiles have received comparatively little attention. Crocodylians are particularly vulnerable to Hg contamination due to their life history, being long-lived, high-trophic predators with relatively low metabolic and high tissue conversion rates, favoring bioaccumulation over a lifetime of several decades (Lemaire, 2023).

To better understand the developmental and endocrine consequences of Hg exposure during egg formation in oviparous vertebrates, we need to evaluate maternal transfer of Hg. In crocodylians, Hg is transferred to eggs during vitellogenesis, linking maternal Hg burden to embryonic exposure in a closed developmental system, making causal inference easier to interpret than with viviparous taxa. Vertical transfer of Hg from the females to their eggs has been demonstrated in American alligators and inferred from hatchling Hg loads in other species (Nilsen et al., 2020; Lemaire et al., 2021a), emphasizing the need to quantify

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https://doi.org/10.1016/j.envres.2026.125508
Received 19 May 2026; Received in revised form 12 August 2026; Accepted 17 August 2026
Available online 18 August 2026

in-ovo exposure and its physiological consequences.

Non-lethal sampling of keratinized tissues (e.g., claws, scutes) provides valuable information on long-term exposure with minimal impact on individuals. The distal portion of hatchling claws represents Hg integrated during embryonic development (i.e., incubation), while Hg incorporated through diet during the first days after hatching would be deposited in the proximal portion of the claw, which therefore can serve as an integrated proxy for embryonic Hg exposure (Lemaire et al., 2021a), offering a practical alternative to destructive egg sampling for evaluating maternal transfer in wild populations, especially for assessing the impacts of early-life exposure to Hg.

Mercury is an endocrine-disrupting chemical capable of interfering with or mimicking steroid hormone signaling and disrupting endocrine axes that regulate reproduction, parental care, and stress physiology (Tan et al., 2009; Wada et al., 2009). In crocodylians, chronic exposure has been linked to alterations in corticosterone (CORT) plasma levels, Hypothalamic Pituitary Adrenal (HPA) axis responsiveness, and liver function, supporting broader inference of endocrine disruption in wild individuals (Lemaire et al., 2021b; Romero-Calderón et al., 2022). Endocrine-organizing effects during embryogenesis are of particular concern as early perturbations of glucocorticoids and sex steroids can shape the development of the HPA axis, with potential implications on growth, behavior, and survival (Groothuis et al., 2005; Dantzer et al., 2013).

The smooth-fronted caiman, *Paleosuchus trigonatus*, is a small-bodied caiman living in the closed canopy rainforests of French Guiana, where ASGM activities are responsible for Hg elevation and bioavailability in the environment. The species is territorial and sedentary, making it a good model to study spatial variation in maternal exposure and transfer to eggs. Building on evidence that hatchling keratin tissues, especially claws, reflect in-ovo Hg exposure and that endocrine function is sensitive to Hg (Lemaire et al., 2021a), we want to evaluate whether maternally transferred Hg is associated with variation in hatchling CORT baseline levels and body condition, two integrative markers of early life stress physiology and energetic allocation.

2. Material and methods

2.1. Sample collection

We sampled 15 *Paleosuchus trigonatus* hatchlings from 4 different nests in 3 different areas in French Guiana between 2022 and 2025 (Fig. 1). Individuals were found and captured near their respective nests and, based on the umbilical cicatrix, were estimated to be < 1 week old. For all individuals, claw and tail scute samples were collected using clean pliers and were placed in dry plastic containers. We drew blood from the occipital cranial vein within 3 min of capture to obtain baseline CORT levels. Blood samples were kept cool and, within 3 h, centrifuged for 5 min at 6500 rpm (1889 rcf) to separate plasma from red blood cells (RBCs). RBCs were then put in separate tubes containing 99% ethanol (HPLC grade) until Hg quantification in the laboratory. To quantify CORT, 50 µl of plasma were transferred to a tube containing 750 µl of 99% ethanol (HPLC grade). Biometrics, including snout-vent length and weight, were recorded for each individual. Neonates were released at the location of capture after sampling.

Paleosuchus trigonatus is protected by the French law (Ministerial decree NOR: TREL1933710 A of October 08, 2018), and a permission to capture individuals, draw blood, and sample claws and scutes was granted by the French authorities (Direction Regionale des Territoires et de la Mer) after evaluation by the CSRPN, the regional scientific committee (Permit: R03-2022-10-20-00004).

2.1.1. Mercury analysis

Before Hg analysis, claw and scute samples were cleaned in an ultrasonic bath and dried according to the method described by Lemaire et al. (2021a). Ethanol from RBC samples was evaporated under a nitrogen stream at room temperature, then the samples were freeze-dried for 48h, ground, and homogenized.

Total Hg (THg) was quantified in all samples by direct measurement of at least two replicas using a Direct Mercury Analyzer (DMA-80 evo III, atomic absorption spectrometer, Milestone®) at the University of Vienna, Austria. Inter-replicate reproducibility for each sample was validated against a relative standard deviation threshold of <10%. The mean concentration of duplicate measurements, was used in subsequent

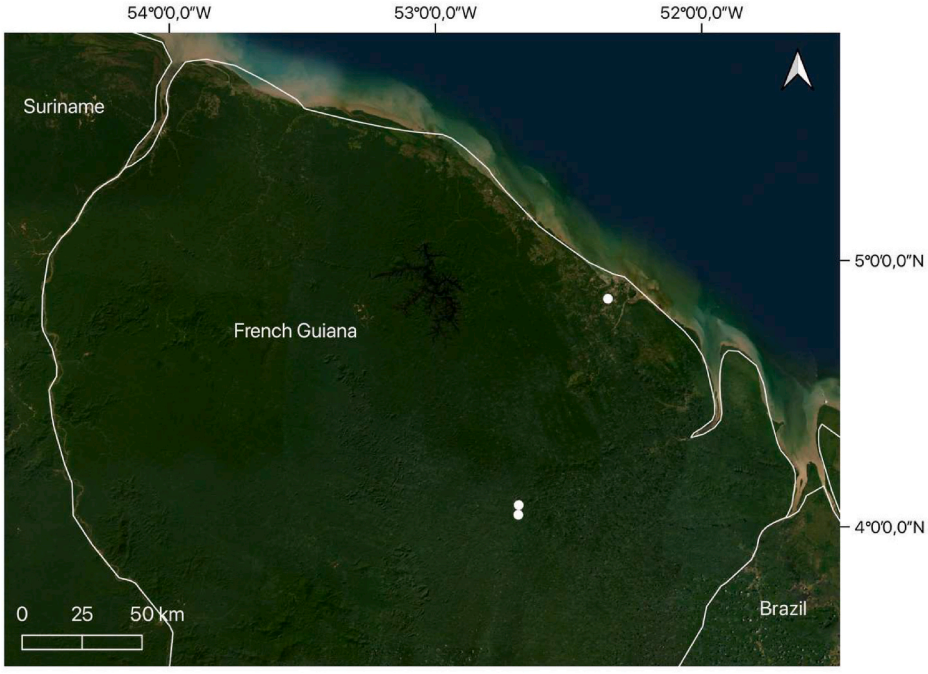

Fig. 1. Geographic locations for the sampled areas of *Paleosuchus trigonatus* hatchlings in French Guiana. Source map: ESRI Satellite.

calculations for samples. The method was validated by analysis of certified reference material (CRM) of TORT-3 (Lobster hepatopancreas, National Research Council of Canada; certified reference Hg concentration: 0.292 ± 0.022 μg g^{-1} dw). CRM was analyzed at the beginning and end of the analytical cycle, and between every ten samples. Measured TORT-3 values were 0.296 ± 0.006 μg g^{-1} dw (n = 10), with a recovery rate of 101.4 ± 2.19%. The detection limit of the DMA-80 was 0.01 ng. Hg concentrations are further expressed in μg.g^{-1} dw (dry weight).

2.1.2. Corticosterone quantification

Samples were quantified following the method described in Goymann et al. (2007).

Samples (50 μl of plasma in 750 μl of ethanol) were brought to room temperature, briefly vortexed, and centrifuged at 3900 rpm (3292 rcf) for 10 min. The supernatant was carefully removed and pipetted into a glass tube. Next, 750 μl of absolute ethanol (96%) was added to the original sample tube, and centrifugation procedure was repeated. The supernatant was combined with the first liquid phase from the same sample, and was then dried under an N_2 stream at 37°C.

For liquid-liquid extraction (LLE), the samples were resuspended in 800 μl of ultrapure water and 4 ml of dichloromethane (HPLC grade) and were then shaken for 4 h at room temperature. Then, samples were centrifuged for 10 min at 3900 rpm (3292 rcf) to separate the organic from the water phases. The organic phase was decanted into a new glass tube using a dry ice bath. After repetition of LLE, the organic phase was combined with the dichloromethane phase from the first LLE. The dichloromethane phase was dried entirely under an N_2 stream at 37°C.

The dry samples were resuspended in assay buffer provided by the ELISA manufacturer (Arbor Assays assay buffer X065). The samples were stored overnight at 4°C until assayed the next day. Samples were quantified with Arbor Assays DetectX® Corticosterone Multi-Format ELISA Kits (Cat. No. K014-H) following the manufacturer's instructions. Samples were corrected for dilution. All samples and standards were measured in duplicate, and the coefficient of variation between duplicate measurements was below 3% for all. The mean concentration of duplicate measurements, corrected for the dilution factor, was used in subsequent calculations for samples. The intra-assay coefficient of variation was 7.1% and 5.9% and the inter-assay coefficient of variation was 11.2% (samples were assayed in two assays using a control sample).

2.1.3. Statistical analysis

All statistical analyses were performed using the software R v.4.4.0 (R core team). We analyzed the relationship between Hg concentrations and CORT levels using a linear regression. Both variables were log-transformed. Log-transformed Hg concentrations for either claws, scutes, or RBCs were included as independent variable and log-transformed CORT concentrations as the response variable. Model diagnostics were visually inspected to verify normality and homoscedasticity of residuals.

To derive a size-dependent index of body condition, body mass and snout-vent length were log-transformed, and a linear regression was used to observe the relationship. The residuals from the model represent individual deviation from expected body mass for a given body size and were used as an index of relative body condition (RBCI). Positive residuals indicate individuals heavier than expected, and negative residuals indicate individuals lighter than expected for their size. This RBCI was used as the response variable in a linear regression with log-transformed CORT concentrations as the explanatory variable to test for an association between physiological stress and body condition. All analyses were performed using linear models. Body condition was quantified using residual body mass to control for allometric effects of body size.

3. Results

Hatchling snout-vent length was 14.5 ± 1.22 cm (Mean ± SD), and body mass was 76.8 ± 16.73 g. THg concentration in the blood (RBCs) was 0.185 ± 0.088 μg g^{-1}, ranging between 0.039 and 0.319 μg g^{-1}; THg concentration in scutes was 0.427 ± 0.261 μg g^{-1} ranging between 0.120 and 1.030 μg g^{-1}; and in claws 0.572 ± 0.171 μg g^{-1} ranging from 0.364 to 0.914 μg g^{-1}. Baseline CORT concentrations in plasma were 5.91 ± 4.31 ng ml^{-1}, ranging from 1.01 to 16.16 ng ml^{-1}.

Results showed a significant positive relationship between baseline plasma CORT and Hg concentration in claws (linear regression; $R^2 = 0.65$, $p < 0.001$; Fig. 2), scutes (linear regression; $R^2 = 0.67$, $p < 0.001$) and RBCs (linear regression; $R^2 = 0.39$, $p = 0.018$).

Mercury concentrations (log-transformed) between all matrices were correlated (linear regression: Claws-Scutes, $R^2 = 0.75$, $p < 0.001$; Scutes-RBCs, $R^2 = 0.77$, $p < 0.001$; Claws-RBCs, $R^2 = 0.75$, $p < 0.001$)

Results showed a positive relationship between log-transformed body mass and log-transformed body size ($R^2 = 0.74$, $p < 0.001$). The residuals from this model were therefore used as RBCI independent of body size. A negative relationship between RBCI and log-transformed CORT was observed (linear regression; $R^2 = 0.48$, $p = 0.004$; Fig. 3), indicating that elevated baseline CORT concentrations were associated with reduced mass relative to body size. No significant relationships were observed between RBCI and log-transformed Hg concentrations for claws (linear regression; $R^2 = 0.10$, $p = 0.289$), scutes (linear regression; $R^2 = 0.16$, $p = 0.161$) or RBCs (linear regression; $R^2 = 0.11$, $p = 0.242$).

4. Discussion

In the present study, Hg concentrations quantified in the claws (0.572 ± 0.171 μg g^{-1}) and scutes (0.427 ± 0.261 μg g^{-1}) of *Paleosuchus trigonatus* hatchlings are consistent with ranges previously described for hatchlings of the same species collected between 2017 and 2020 in French Guiana (Lemaire et al., 2021a). However, these concentrations are relatively low compared to those observed in hatchlings of the Dwarf caiman *Paleosuchus palpebrosus* and the Spectacled caiman *Caiman crocodilus* in French Guiana (up to 1.379 μg g^{-1} at 14.4 cm SVL and up to 1.165 μg g^{-1} at 14.5 cm SVL in claws, respectively; unpublished data).

The positive relationship between keratinized tissue Hg concentrations and plasma CORT levels in hatchlings may indicate that prenatal Hg exposure is responsible for the alteration of CORT levels.

Hatchling claws are primarily composed of alpha-keratin, which is richer in cysteine and disulfide bonds compared to beta-keratin that composes the scutes. This composition facilitates the accumulation of Hg (mainly as MeHg) to the thiol residues of cysteines, where Hg binds to -SH groups (Alibardi et al., 2007; Toni et al., 2007). Due to this characteristic, hatchling claws and scutes slowly accumulate Hg during formation and can serve as a proxy of the overall embryonic exposure related to maternally transferred Hg (Lemaire et al., 2021a). Keratinized tissues can therefore help to evaluate embryonic exposure to Hg in oviparous species such as birds and reptiles. In birds and crocodylians, vitellogenesis is controlled by hepatic synthesis, which is fueled by dietary intake, adipose tissue, and muscle protein (Price, 2017; Chacón et al., 2024). During vitellogenesis, MeHg is the primary transferred form of Hg due to thiol binding to vitellogenin and lipovitellins, which provide abundant binding sites. Additionally, studies quantifying MeHg in eggs support the finding that bird eggs contain more than 90% of their total Hg in the MeHg form (Ackerman et al., 2013). Nilsen et al. (2020) showed that maternal transfer from the female to the eggs represents approximately 12.8% of the blood Hg burden of the female American alligator, *Alligator mississippiensis*, highlighting the direct link between female contamination and Hg being maternally transferred to the eggs.

Besides contaminants, other essential chemicals are maternally transferred during egg formation, such as steroids, including corticosteroids (Groothuis et al., 2019). During vitellogenesis, the quantity of glucocorticoids transferred to the yolk varies depending on the

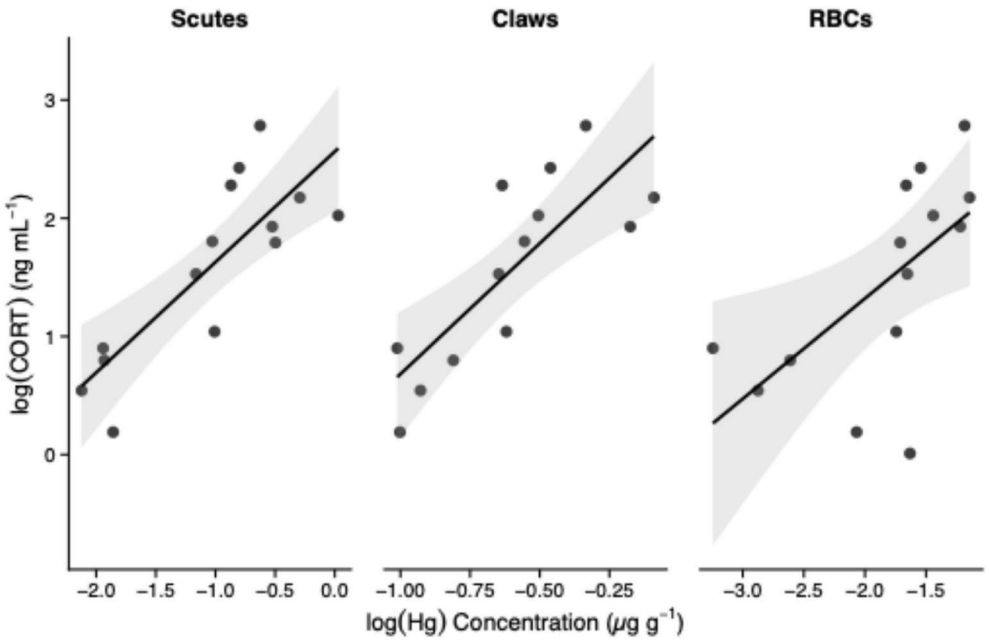

Fig. 2. Population-level relationship between plasma corticosterone concentration (log CORT in ng.ml^{-1}) and mercury concentrations in tail scutes, claws and red blood cells (RBCs) (log Total Hg in μg.g^{-1} dw) of hatchling Smooth-fronted caimans (*Paleosuchus trigonatus*) in French Guiana (Linear regression: Scutes $R^2 = 0.67$, $p < 0.001$; Claws $R^2 = 0.65$, $p < 0.001$; RBCs $R^2 = 0.39$, $p = 0.018$).

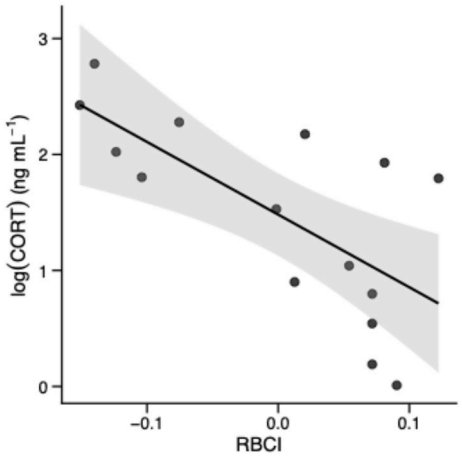

Fig. 3. Relationship between plasma corticosterone concentration (log CORT in ng.ml^{-1}) and index of relative body condition (RBCI) of hatchling Smooth-fronted caimans (*Paleosuchus trigonatus*) in French Guiana (linear regression: $R^2 = 0.48$, $p = 0.004$).

environmental conditions experienced by the female (Groothuis et al., 2019). It is likely that poor environmental conditions act as a stressor, resulting in females having higher circulating levels of glucocorticoids which in turn causes the transfer of a greater quantity of glucocorticoids to the yolk. Elevations in circulating female glucocorticoids may not only lead to direct transfer of these hormones but could indirectly suppress maternal nutrient provisioning (Henriksen et al., 2011). Previous work has shown that high maternal corticosteroid levels influence hatchling phenotypes and reduce hatchling size and weight in birds (Janczak et al., 2006; Henriksen et al., 2013; Ahmed et al., 2014).

Elevated CORT levels in the yolk influence the responsiveness of hatchlings to stressors (Hayward and Wingfield, 2004; Zimmer et al., 2013) but do not necessarily lead to an increase in baseline CORT of hatchlings (Henriksen et al., 2013). Elevated baseline CORT concentration in certain conditions may be physiologically costly; this pattern, along with poor body condition, could significantly reduce overall survival.

Exposure to endocrine-disrupting chemicals, such as MeHg, during embryogenesis can have several deleterious effects for embryonic development and hatchling survival, especially in precocial animals (Heinz et al., 2009; Ottinger et al., 2008). Elevated CORT concentrations in relation to low RBCI ($R^2 = 0.48$, $p = 0.004$) observed in our study in hatchlings exposed to higher in-ovo Hg concentrations may reflect alteration of embryonic energy allocation due to endocrine disruption. During embryonic development, the proper use of egg reserves - particularly the yolk in crocodylians - is essential for embryonic development (Nelson et al., 2010). Mercury can interfere with metabolic and endocrine pathways that regulate yolk allocation, thereby increasing the energetic costs for metabolic maintenance (Basu, 2023). The regulation of embryonic metabolism and reserve mobilization is highly controlled by CORT (Hayward and Wingfield, 2004). Consequently, an alteration in HPA axis sensitivity due to Hg contamination can promote catabolic processes at the expense of tissue formation via elevated CORT concentrations.

Additionally, Hg is known to disrupt thyroid hormone signaling (Wada et al., 2009; Hernandez-Gonzalez et al., 2025), which may further alter metabolic rate and the timing of reserve use during embryonic development, reducing the efficiency in yolk-to-tissue conversion. This could explain the observed pattern of reduced body condition and elevated CORT concentrations in hatchlings.

Furthermore, mercury's capacity to mimic estrogenic actions may explain the results observed in our study. Research has shown that Hg can modulate estrogen receptor signaling and steroidogenic pathways (Tan et al., 2009), which are key regulators of HPA axis activity. Enhanced estrogenic signaling during development can increase hypothalamic corticotropin-releasing hormone (CRH) expression and attenuate glucocorticoid negative feedback, resulting in elevated baseline CORT levels.

The interaction between estrogen and glucocorticoids influences metabolic allocation, leading to the shift of energy use toward maintenance and catabolism rather than somatic tissue formation. Such alteration during embryonic development leads to reduced fitness and potentially lower hatchling survival (Dayananda et al., 2017). Elevated

CORT may lead to a behavioral trade-off by increasing the flight response to predators or by altering the time budget for foraging or exploration (Wada and Breuner, 2008; Uller et al., 2009; Possenti et al., 2018).

Furthermore, Elsey et al. (1990) showed that elevated CORT concentrations reduced growth rates in *Alligator mississippiensis*. While some species can "catch up" by accelerating growth over several weeks, the physiological costs of these mechanisms can have long-term negative consequences (Metcalfe and Monaghan, 2001). Additionally, previous studies by Johnson et al. (2023a, 2023b) showed a potential confounding influence of incubation temperature on hatchling blood Hg levels, body condition, and survival, which may have played an additional role.

While our results demonstrate a clear transgenerational effect of Hg contamination, the potential long-term impacts on individuals require further investigation. Specifically, it is necessary to assess whether elevated glucocorticoid levels during development have lasting effects on reproductive strategies and brain development in caimans.

5. Conclusion

Results of this study highlight the significance of maternal transfer as a pathway for mercury contamination in *Paleosuchus trigonatus* hatchlings. Although Hg concentrations in this species remain lower than those observed in sympatric caimans like *Paleosuchus palpebrosus* and *Caiman crocodilus*, the strong positive correlation between Hg in keratinized tissues and plasma CORT levels suggests that even low Hg levels can have effects during embryonic development. The accumulation of MeHg in keratinized tissues, such as claws and scutes, provides a reliable proxy for non-invasively assessing in-ovo hatchling exposure.

Furthermore, this exposure appears to alter the HPA-axis. Elevated CORT levels can redirect energy away from somatic growth and toward catabolic maintenance, resulting in hatchlings with reduced body condition. Ultimately, these transgenerational effects highlight the vulnerability of crocodylian hatchlings to Hg exposure during embryonic development. While some individuals may exhibit compensatory growth, the long-term consequences for reproductive strategy, cognitive development, and overall survival probability remain critical areas for future investigation.

CRediT authorship contribution statement

Jérémy Lemaire: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Rosanna Mangione:** Investigation, Writing – original draft, Writing – review & editing. **Leonida Fusani:** Writing – original draft, Writing – review & editing. **Virginie Canoine:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jeremy Lemaire reports financial support was provided by Austrian Science Fund. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was funded by the Austrian Science Fund (FWF) [10.55776/ESP408], which is attributed to J. Lemaire.

We want to thank the teams of the nature reserves 'Nouragues" and "Mont-Grand Matoury" in French Guiana for their logistical and field assistance. We thank the Nouragues Research Field Station (managed by the CNRS), which benefits from "Investissement d'Avenir" grant managed by the Agence National de la Recherche (AnaEE France ANR-11-INBS-0001; Labex CEBA ANR-10-LABX-25-01). We thank Caroline Deimel for helping with hormone analyses. For open access purposes, the author has applied a CC BY public copyright license to any author-accepted manuscript version arising from this submission.

Data availability

Data will be made available on request.

References

Ackerman, J.T., Herzog, M.P., Schwarzbach, S.E., 2013. Methylmercury is the predominant form of Mercury in bird eggs: a synthesis. Environ. Sci. Technol. 47 (4), 2052–2060.

Ahmed, A.A., Ma, W., Ni, Y., Zhou, Q., Zhao, R., 2014. Embryonic exposure to corticosterone modifies aggressive behavior through alterations of the hypothalamic pituitary adrenal axis and the serotonergic system in the chicken. Horm. Behav. 65, 97–105.

Alibardi, L., Toni, M., Dalla Valle, L., 2007. Hard cornification in reptilian epidermis in comparison to cornification in Mammalian epidermis. Exp. Dermatol. 16 (12), 961–976.

Basu, M., 2023. Impact of mercury and its toxicity on health and environment: a general perspective. In: Kumar, N. (Ed.), Mercury Toxicity. *Environ. Sci. Eng.* Springer, Singapore.

Benoit, J.M., Gilmour, C.C., Heyes, A., Mason, R.P., Miller, C.L., 2003. Geochemical and biological controls over methylmercury production and degradation in aquatic ecosystems. Am. Chem. Soc. Symp. Ser. 835, 262–297.

Bridges, K.N., Soulen, B.K., Overturf, C.L., Drevnick, P.E., Roberts, A.P., 2016. Embryotoxicity of maternally transferred methylmercury to fathead minnows (*Pimephales promelas*). Environ. Toxicol. Chem. 35, 1436–1441.

Chacón, C.F., Parachú Marcó, M.V., Poletta, G.L., Siroski, P.A., 2024. Lipid metabolism in crocodilians: a field with promising applications in the field of ecotoxicology. Environ. Res. 252, 119017.

Crowe, W., Allsopp, P.J., Watson, G.E., Magee, P.J., Strain, J.J., Armstrong, D.J., McSorley, E.M., 2017. Mercury as an environmental stimulus in the development of autoimmunity – a systematic review. Autoimmun. Rev. 16, 72–80.

Dantzer, B., Newman, A.E.M., Boonstra, R., Plame, R., Boutin, S., Humphries, M.M., McAdam, A.G., 2013. Density triggers maternal hormones that increase adaptative offspring growth in a wild mammal. Science 340, 1215–1217.

Dayananda, B., Penfold, S., Webb, J.K., 2017. The effects of incubation temperature on locomotor performance, growth and survival in hatchling velvet geckos. J. Zool. 303, 46–53.

Driscoll, C.T., Mason, R.P., Chan, H.M., Jacob, D.J., Pirrone, N., 2013. Mercury as a global pollutant: sources, pathways, and effects. Environ. Sci. Technol. 47, 4967–4983.

Eagles-Smith, C.A., Silbergeld, E.K., Basu, N., Bustamante, P., Diaz-Barriga, F., Hopkins, W.A., Kidd, K.A., Nyland, J.F., 2018. Modulators of Mercury risk to wildlife and humans in the context of rapid global change. Ambio 47, 170–197.

Elsey, R.M., Joanen, T., McNease, L., Lance, V., 1990. Growth rate and plasma corticosterone levels in juvenile alligators maintained at different stocking densities. J. Exp. Zool. 255, 30–36.

GMA, 2019. "Global Mercury Assessment 2018" (UN Environmental Programme. Chemicals and Health Branch Geneva, Switzerland.

Goymann, W., Schwabl, I., Trappschuh, M., Hau, M., 2007. Use of ethanol for preserving steroid and indoleamine hormones in bird plasma. Gen. Comp. Endocrinol. 150 (2), 191–195.

Groothuis, T.G.G., Hsu, B.-Y., Kumar, N., Tschirren, B., 2019. Revisiting mechanisms and functions of prenatal hormone-mediated maternal effects using avian species as a model. Philos. Trans. R. Soc. B 374, 20180115.

Groothuis, T.G.G., Müller, W., von Engelhardt, N., Carere, C., Eising, C., 2005. Maternal hormones as a tool to adjust offspring phenotype in Avian species. Neurosci. Biobehav. Rev. 29 (2), 329–352.

Hayward, L.S., Wingfield, J.C., 2004. Maternal corticosterone is transferred to Avian yolk and may alter offspring growth and adult phenotype. Gen. Comp. Endocrinol. 135 (3), 365–371.

Heinz, G.H., Hoffman, D.J., Klimstra, J.D., Stebbins, K.R., Konrad, S.L., Erwin, C.A., 2009. Species differences in the sensitivity of avian embryos to methylmercury. Arch. Environ. Contam. Toxicol. 56, 129–138.

Henriksen, R., Rettenbacher, S., Groothuis, T.G.G., 2011. Prenatal stress in birds: pathway, effects, function and perspectives. Neurosci. Biobehav. Rev. 35, 1384–1501.

Henriksen, R., Rettenbacher, S., Groothuis, T.G.G., 2013. Maternal corticosterone elevation during egg formation in chickens (*Gallus gallus domesticus*) influences offspring traits, partly via prenatal undernutrition. Gen. Comp. Endocrinol. 191, 83–91.

Hernandez-Gonzalez, M., Eens, M., Chastel, O., Costantini, D., Sebatiano, M., 2025. Meta-analytical evidence for the endocrine-disrupting properties of mercury exposure in wild birds. Sci. Total Environ. 991, 179969.

Hopkins, B.C., Willson, J.D., Hopkins, W.A., 2013. Mercury exposure is associated with negative effects on turtle reproduction. Environ. Sci. Technol. 47, 2416–2422.

Janczak, A.M., Braastad, B.O., Bakken, M., 2006. Behavioural effects of embryonic exposure to corticosterone in chickens. Appl. Anim. Behav. Sci. 92, 69–82.
Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Dìaz, S., Molnár, Z., Purvis, A., 2022. The direct drivers of recent global anthropogenic biodiversity loss. Sci. Adv. 8, eabm9982.
Johnson, J.M., Bock, S.L., Smaga, C.R., Lambert, M.R., Rainwater, T.R., Wilkinson, P.M., Parrott, B.B., 2023b. Relationships between maternally-transferred mercury and hatchling development, behavior, and survival in the American alligator (Alligator mississippiensis). Sci. Total Environ. 870, 162010.
Johnson, J.M., Smaga, C.R., Bock, S.L., Parrott, B.B., 2023a. Maternal provisioning interacts with incubation temperature to affect hatchling mercury exposure in an oviparous reptile. Biol. Lett. 19 (8), 20230097.
Landler, L., Painter, M.S., Coe, B.H., Youmans, P.W., Hopkins, W.A., Phillips, J.B., 2017. High levels of maternally transferred mercury disrupt magnetic responses of snapping turtle hatchlings (*Chelyda serpentina*). Environ. Pollut. 11, 19–25.
Lemaire, J., 2023. Using crocodylians for monitoring mercury in the tropics. Ecotoxicology 32, 977–993.
Lemaire, J., Bustamante, P., Mangione, R., Marquis, O., Churlaud, C., Brault-Favrou, M., Parenteau, C., Brischoux, F., 2021b. Lead, mercury, and selenium alter physiological functions in wild caimans (*Caiman crocodilus*). Environ. Pollut. 286, 117549.
Lemaire, J., Marquis, O., Bustamante, P., Mangione, R., Brischoux, F., 2021a. I got it from my mother: inter-nest variation of mercury concentration in neonate Smooth-fronted Caiman (*Paleosuchus trigonatus*) suggests maternal transfer and possible phenotypical effects. Environ. Res. 194, 110494.
Metcalfe, N.B., Monoghan, P., 2001. Compensation for a bad start: grow now, pay later? Trends Ecol. Evol. 16 (4), 254–260.
Nelson, T.C., Groth, K.D., Sotherland, P.R., 2010. Maternal investment and nutrient use affect phenotype of American alligator and domestic chicken hatchlings. Comp. Biochem. Physiol. Mol. Integr. Physiol. 157, 19–27.
Nilsen, F.M., Rainwater, T.R., Wilkinson, P.M., Brunell, A.M., Lowers, R.H., Bowden, J. A., Guillette, L.J., Long, S.E., Schock, T.B., 2020. Examining maternal and environmental transfer of mercury into American alligator eggs. Ecotoxicol. Environ. Saf. 189, 110057.
Ottinger, M.A., Lavoie, E., Thompson, N., Barton, A., Whitehouse, K., Barton, M., Abdelnabi, M., Quinn Jr., M., Panzica, G., Viglietti-Panzica, C., 2008. Neuroendocrine and behavioral effects of embryonic exposure to endocrine disrupting chemicals in birds. Brain Res. Rev. 57 (2), 376–385.
Podar, M., Gilmour, C.C., Brandt, C.C., Soren, A., Brown, S.D., Crable, B.R., Palumbo, A. V., Somenahally, A.C., Elias, D.A., 2015. Global prevalence and distribution of genes and microorganisms involved in mercury methylation. Sci. Adv. 1 (9), e1500675.
Possenti, C.D., Parolini, M., Romano, A., Caprioli, M., Rubolini, D., Saino, N., 2018. Effect of yolk corticosterone on begging in the yellow-legged gull. Horm. Behav. 97, 121–127.
Price, E.R., 2017. The physiology of lipid storage and use in reptiles. Biol. Rev. 92 (3), 1406–1426.
Qiu, X., Liu, M., Zhang, Y., Zhang, Q., Lin, H., Cai, X., Li, X., Dai, R., Zheng, S., Wang, J., Zhu, Y., Shen, H., Shen, G., Wang, X., Tao, S., 2025. Declines in anthropogenic mercury emissions in the Global North and China offset by the Global South. Nat. Commun. 16, 1179.
Romero-Calderlón, A.G., Alvarez-Legorreta, T., von Osten, J.R., González-Jáuregui, M., Cedeño-Vázquez, J.R., 2022. Stress responses in captive Crocodylus moreletii associated with metal exposure. Environ. Pollut. 308, 119685.
Tan, S.W., Meiller, J.C., Mahaffey, K.R., 2009. The endocrine effects of mercury in humans and wildlife. Crit. Rev. Toxicol. 39 (3), 228–269.
Tartu, S., Goutte, A., Bustamante, P., Angelier, F., Moe, B., Clément-Chastel, C., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2013. To breed or not to breed: endocrine response to mercury contamination by an Arctic seabird. Biol. Lett. 9, 20130317.
Toni, M., Dalla Valle, L., Alibardi, L., 2007. Hard(Beta-)Keratins in the epidermis of reptiles: composition, sequence, and molecular Organization. J. Proteome Res. 6 (9), 3377–3392.
Uller, T., Hollander, J., Astheimer, L., Olsson, M., 2009. Sex-specific developmental plasticity in response to yolk corticosterone in an oviparous lizard. J. Exp. Biol. 212 (8), 1087–1091.
Wada, H., Breuner, C.W., 2008. Transient elevation of corticosterone alters begging behavior and growth of white-crowned sparrow nestlings. J. Exp. Biol. 211, 1696–1703.
Wada, H., Cristol, D.A., McNabbs, F.M.A., Hopkins, W.A., 2009. Suppressed adrenocortical responses and thyroid hormone levels in birds near a mercury-contaminated river. Environ. Sci. Technol. 43 (15), 6031–6038.
Zhang, Q.F., Li, Y.W., Liu, Z.H., Chen, Q.L., 2016. Exposure to mercuric chloride induces developmental damage, oxidative stress and immunotoxicity in zebrafish embryos-larvae. Aquat. Toxicol. 181, 76–85.
Zimmer, C., Boogert, N.J., Spencer, K.A., 2013. Developmental programming: cumulative effects of increased pre-hatchling corticosterone levels and post-hatching unpredictable food availability on physiology and behavior in adulthood. Horm. Behav. 64 (3), 495–500.