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CADMIUM DOES NOT AFFECT POST-HATCHING MATERNAL CARE OR EARLY OFFSPRING DEVELOPMENT IN EARWIGS

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Lay summary

The ingestion of cadmium by earwig mothers and juveniles does not affect the expression of post-hatching maternal care. It did not affect the early development of offspring but increased the expression of self-grooming by mothers. Overall, these findings show that heavy metal contaminations do not necessarily shape parent-offspring interactions. They also raise fundamental questions about the underlying mechanisms that mediate the tolerance, resistance and/or detoxification of cadmium in this insect.

Abstract

Anthropogenic pollution is steadily increasing and has a major impact on biodiversity. Chemical pollutants in particular affect many reproductive, physiological and survival traits in a wide range of organisms. However, the effects on behavioural traits have been less studied, although they could have wide-ranging negative effects from the individual to the community level. Here, we attempted to fill this knowledge gap by investigating the effect of a common heavy metal pollutant, cadmium, on post-hatching maternal care and juvenile development in the European earwig *Forficula auricularia*. We fed 108 earwig families with five different cadmium concentrations (0, 12.5, 25, 50 and 100 mg.L⁻¹), and measured ten parameters related to offspring care, non-care maternal behaviours, investment in maternal care and two parameters of offspring development (offspring weight gain and survival). Somewhat surprisingly, we found no effect of cadmium ingestion on any of the parameters measured, except for maternal self-grooming behaviour. In particular, the ingestion of cadmium by group members did not result in an overall decrease in the expression of care by the contaminated mothers or in an overall higher level of care received by the contaminated offspring. By contrast, mothers fed the highest dose of cadmium showed an increase in self-grooming, probably due to the stress of toxic ingestion. Overall, our study raises questions about whether and how parent-offspring interactions can alter the negative effects of contaminated environments in social species.

Keywords: Anthropogenic change; Parent-offspring interactions; Insect; Parental care; Trace metal.

Introduction

The recent development of agriculture and industry has led to an exponential increase in environmental pollution, whether acoustic (Alquezar et al. 2020; Bowen et al. 2020), light (Caorsi et al. 2019; Elgert et al. 2021), or chemical (Ringot et al. 2018; Goretti et al. 2020). The major impact of such anthropogenic pollution on altering ecosystem functioning, biodiversity and natural populations dynamics (Dirzo et al. 2014) has long been studied through its effects on the survival, reproduction and physiology in a wide variety of animals (e.g. Gomot 1998; Jacquin et al. 2020; Su et al. 2021). By comparison, the diversity and importance of the effects of anthropogenic pollution on animal behaviour remain poorly investigated (Bertram et al. 2022). This is surprising, as an inability to produce or maintain a behaviour can lead to a long-term cascade of negative effects at both the individual and community levels (Saaristo et al. 2018; Candolin and Wong 2019). For instance, exposure to anthropic pollution in the form of non-lethal doses of pesticides affects learning, mating success and the escape from predators in many taxa from fish to humans (review in Zala and Penn 2004), which in turn can alter survival, reproductive rates and population maintenance (Dew et al. 2014; Luo et al. 2020). This limited attention to behaviours is also surprising because behaviours can be useful biomarkers for measuring the effects of pollution over short periods of time. For example, the presence of low doses of an aquatic pollutant (benzoprene) in the water could be detected by measuring the level of anxiety-like behaviour in zebrafish just 30 minutes after exposure (Hamilton et al. 2021).

Among the behaviours that can affect the fitness of an individual, the effects of anthropogenic pollution on social behaviours, such as parental care, may be particularly important to look at (see Aulsebrook et al. 2020). These taxonomically widespread behaviours (Trumbo 2013; Meunier et al. 2022; Mock 2022; Vági et al. 2022) can indeed spread the effects of anthropic pollution (or the pollutants themselves) on one individual to all group members. For instance, in honeybees, social behaviour mediates the transmission of contaminated food and chemical pollutants among colony members (Monchanin et al. 2021) and to the larvae in development (Leita et al. 1996). Moreover, parental care is often sensitive to even subtle environmental perturbations, which in turn can amplify their effects on the fitness of juveniles. For example, exposure to continuous or intermittent light pollution alters the level of parental care in the smallmouth bass *Micropterus dolomieu* (Foster et al. 2016), and rat mothers fed with pesticide-contaminated food (lindane) exhibited a lack of retrieval behaviour and consequential litter loss (Matsuura et al. 2005). Nevertheless, anthropic pollution does not always reduce the expression of parental care, as mothers exposed to a glyphosate-based herbicide show a higher expression of licking behaviours toward pups in rats (Dechartres et al. 2019).

The effects of chemical pollution on parental care are less clear when considering exposure to non-pesticidal compounds, including trace metals such as zinc, lead, mercury and cadmium. Cadmium, in particular, is one of the most toxic and mobile chemical elements in the environment (Kubier et al. 2019). Almost all living organisms are expected to ingest this compound during their lifetime, because it tends to bioaccumulate throughout the food chain (Butt et al. 2018; Dutta et al. 2019; Zhang and Reynolds 2019) and because its concentration in groundwater and soil continuously increases due to human activities (such as fossil fuel exploitation, road traffic and agriculture - review in Kubier et al. 2019; Zhang and Reynolds 2019). A growing number of studies show that cadmium ingestion can affect the physiology, development and reproduction of several species (e.g. Cervera et al. 2004;

Malakar et al. 2009; Li et al. 2018; Luo et al. 2020; Honorio et al. 2021). However, its effects on behaviour, and especially parental care, are still poorly understood and are sometimes contradictory. On one hand, studies show that cadmium ingestion can have detrimental effects on the expression of certain behaviours such as aggression in rats (Arito et al. 1981), locomotion in the common fruit fly *Drosophila melanogaster* (Nanda and Firdaus 2022) and mating behavior in the Asian corn borer *Ostrinia furnacalis* and the beet armyworm *Spodoptera exigua* (Luo et al. 2020; Su et al. 2021). On the other hand, a recent study did not detect an effect of cadmium ingestion on the expression of maternal care toward eggs and egg hatching rate in the European earwig (Honorio et al. 2023). However, it remains unclear whether cadmium ingestion by earwig mothers and their juveniles after egg hatching can alter social interactions during family life and may thus have a strong impact on the fate of juveniles at the end of this period.

In this study, we followed up on Honorio et al. (2023) and investigated whether cadmium ingestion by mothers and newly-hatched juveniles alters the expression of post-hatching maternal care, as well as the development and survival of offspring during the period of care in the European earwig. There were two main reasons why we expected a different effect of cadmium on the expression of pre- and post-hatch care in this species. First, the physiological state of earwig mothers typically varies between pre- and post-hatching phases (Rankin et al. 1995), and previous studies revealed that it may result in a stage-specific sensitivity to chemical pollution. For instance, *F. auricularia* mothers exposed to a pesticide (deltamethrin) just after oviposition showed a reduced expression of egg care (Meunier et al. 2020), whereas earwig mothers exposed to the same pesticide after egg hatching did not modify their expression of juvenile care (Mauduit et al. 2021). Second, post-hatching maternal care, unlike pre-hatching care, is driven by both mothers and juveniles (Kölliker et al. 2015; Wu et al. 2020), and because earwig juveniles partly feed for themselves during parent-offspring interactions (Wong and Kölliker 2012), the level of post-hatching maternal care should at least partly reflect juveniles' exposure to cadmium. Hence, we predicted that mothers would increase their expression of care towards contaminated juveniles compared to non-contaminated juveniles if maternal care helps to protect juveniles from harsh conditions. In contrast, we predicted that mothers would reduce their expression of post-hatching care if cadmium ingestion altered female physiology.

We fed 108 earwig families (consisting of a mother and 10 nymphs) with food supplemented with cadmium at one of five different concentrations. To ensure that mothers' ingested enough cadmium, we fed them both before egg laying and after egg hatching, in the same concentrations throughout the experiment. We measured the expression of three forms of post-hatching maternal care (antennation, grooming and defence) and one proxy of maternal investment in juvenile care (maternal weight change) during the 14 days of parent-offspring interactions. To determine whether these putative effects on maternal care translate into effects of cadmium on other life-history traits in mothers and juveniles (called nymphs), we also measured four female behaviours that are not related to maternal care (self-grooming, exploration, inactivity, distance walked), two proxies of mothers' foraging and digestive activities (food consumption, feces production), the survival rate of mothers, as well as the survival and relative weight gain of nymphs during the period of parent-offspring interactions.

Material and methods

Biological model, rearing conditions and social environment

This study involved 108 *F. auricularia* females (species “A”; Wirth et al. 1998; González-Miguéns et al. 2020) field sampled in July 2021 in peach orchards near Valence, France (Lat 44.9772790, Long 4.9286990). From field sampling to egg hatching, we used the standard rearing conditions detailed in Honorio et al. (2023). In brief, we maintained field-sampled females and males in large containers (32 x 20 x 16.5 cm) until the end of October 2021. At that time, we isolated females in individual Petri dishes (5.5 cm diameter, 1.3 cm height) furnished with moistened sand and maintained at 13°C under constant darkness to trigger egg production. From field sampling to oviposition, each mother received 50mg of homemade food. This food had the same composition as in Kramer et al. 2015 (i.e. mainly pollen, cat food, carrots, and agar), but without the food preservatives sorbic acid and ascorbic acid (not useful in this study as we changed the food twice a week). About 50 days before oviposition (mean \pm SD = 48.3 \pm 20.9 days; min = 20 days), we started to mix the food with one of five concentrations of cadmium (see details below) and changed it twice a week until egg production. On that day, we stopped providing earwig mothers with food (and cadmium) as they stop their foraging activity during the period of egg care (which typically lasts for about 50 days; Kölliker 2007). The same concentration of cadmium was constantly administered throughout the experiment for each family, i.e. to the mother before egg laying and to the mother and nymphs after hatching.

One day after egg hatching, we weighed each mother and 10 arbitrarily chosen nymphs of their respective brood, and then used these individuals to set up 108 experimental families with a trimmed clutch size of 10 nymphs (mean original clutch size \pm SD= 44.7 \pm 14.8 nymphs). We chose to standardise the clutches to 10 nymphs in order to quantify potential differences in the amount of care provided and to exclude the very few clutches of less than 10 nymphs, as these are often produced by females of inherently poor quality (Meunier et al. 2012). We conducted all weighing to the nearest 0.01 mg using a microbalance (OHAUS® Discovery DV215CD). We transferred each experimental family into a large Petri dish (9 cm diameter, 2 cm height), furnished with moistened sand and maintained at 20-18°C under a 12:12h Light:Dark cycle. We provided each family with a standard amount of homemade food (see above) mixed with one of five concentrations of cadmium (see details below).

Cadmium exposure

To manipulate cadmium exposure, we applied 10 μ L of a cadmium solution directly to the 50mg of food provided to each family. We chose cadmium exposure through ingestion because it is considered the main source of cadmium exposure in nature (e.g. Zhang and Reynolds 2019). We applied one of five concentrations of cadmium (0, 12.5, 25, 50 or 100 mg.L⁻¹; respectively resulting in 0, 2.5, 5, 10 and 20 mg.kg⁻¹ of food), which were obtained by using pure MilliQ water or by diluting cadmium chloride powder (Sigma-Aldrich #202908, CAS number: 10108-64-2, purity: 99.99%) in MilliQ water, respectively. We chose these concentrations to cover both the concentrations found in the food chain and soil (e.g. FitzGerald and Roth 2015; Butt et al. 2018; Zhang and Reynolds 2019) as well as those known to induce behavioural changes after ingestion in other insect species (Dési et al. 1998; Su et al. 2021). For instance, in the soil (where earwigs hide in winter), cadmium

concentrations range from 0.1 to 34 mg/kg in Europe (with most values between 1 and 10 mg/kg; FitzGerald & Roth, 2015) and from 0.12 to 1.48 mg/kg in Asia (reviewed in Zhang & Reynolds, 2019). We renewed the cadmium-exposed food every three days for each family until day 14, which is the end of earwig parent-offspring interactions (Kölliker 2007; Kramer et al. 2017). Each family was fed *ad libitum* with the same concentration of cadmium as the mothers were fed about 50 days preceding oviposition. At each change of food, we checked whether at least part of it had been consumed by the individuals. This was always the case. We have previously shown by quantifying cadmium in male earwigs that the ingestion of cadmium under the described conditions did allow the exposure and storage of cadmium within individuals (Honorio et al. 2023). Overall, we fed 21, 21, 22, 22 and 22 experimental families with 0, 12.5, 25, 50 or 100mg.L⁻¹ of cadmium, respectively.

Measurements of mothers' behaviors, foraging activities and survival

During the 14 days of parent-offspring interactions, we tested the effects of cadmium on (1) three forms of post-hatching maternal care (nymph antenation, nymph grooming and nymph defense) and (2) one proxy of maternal investment in nymph care (weight change during the 14 days of parent-offspring interactions). We also measured (3) four maternal behaviors that are not related to nymph care (self-grooming, exploration, inactivity, distance walked), (4) two proxies of mothers' foraging activities (food consumption and feces production), and (5) the survival rate of mothers. In the following section, we will present these measurements in the chronology in which they have been taken.

We first measured the level of maternal food consumption on day six after egg hatching (Mauduit et al. 2021). This measurement started by removing the food in each Petri dish five days after egg hatching. On day six, we deposited each mother in a Petri dish (3.5 cm diameter, 1.2 cm height) containing one pollen pellet that was previously weighed. Two hours later, we weighed the rest of the pollen pellet and returned each mother to her original Petri dish with nymphs. We defined the amount of pollen consumed by each mother as the difference in the weight of the pollen pellet between the two measurements. To deal with uncontrolled variation in the fresh weight of pollen pellets due to air humidity, we added a control treatment (hereafter called "Ct"; n = 22) in which we weighed pollen pellets under the same conditions but without mothers. This allowed us to confirm that all the mothers had consumed the pollen pellets, as the overall weight loss of the pollen pellets was lower in the absence than in the presence of a mother for each treatment (Effect of treatment on pellet weight loss; Linear model, $F_{5,118} = 2.96$, $P = 0.015$; Post-hoc tests - Ct vs Cd 0: $t = 3.73$, $df = 118$, $P = 0.003$; Ct vs Cd 12.5: $t = 3.21$, $df = 118$, $P = 0.020$; Ct vs Cd 25: $t = 3.48$, $df = 118$, $P = 0.020$; Ct vs Cd 50: $t = 3.51$, $df = 118$, $P = 0.008$; Ct vs Cd 100: $t = 2.96$, $df = 118$, $P = 0.041$).

We then measured the level of maternal brood defence on day seven after egg hatching. Maternal brood defence reflects the mother's willingness to protect her nymphs from a simulated predator attack (Thesing et al. 2015). To conduct this measurement, we gently opened each Petri dish, standardly poked each female on the pronotum with soft forceps (one poke per second) and then recorded the number of pokes required until the female moved more than one body length away from her initial position.

We recorded the distance walked by mothers in a new environment on day eight after hatching. We isolated each mother in a plastic circle apparatus (8cm diameter, 5mm

height) fixed between two glass sheets and then filmed her behavior for 15 min (Camera: BASLER BCA 1300, Germany; Media Recorder v4.0, Noldus Information Systems, Netherland). We then analyzed the resulting videos using the software Ethovision XT 16 (Noldus Information Systems, Netherland), in which we extracted the total distance walked by each mother during the 15 min recording.

We measured mothers' behavior and interactions between mothers and nymphs on day eight, just after we recorded the distance walked by mothers. While the mothers were held in the circle apparatus for the video recording described above, their 10 nymphs were gently placed in another apparatus consisting of three arenas (4cm diameter, 3.5mm height) connected by small corridors (4.5mm) in a triangular shape. At the end of the first video, the mother was transferred to this arena, which was then video recorded for the following 25 min. In these 25-min videos, we measured the total duration of mothers' self-grooming, exploration, and inactivity. These behaviors were, respectively, defined as the total amount of time each mother spent on cleaning herself with her mouthparts (a behavior often used to remove dirt or external parasites and to apply protective chemical substances on the cuticle; (Weiß et al. 2014), on being mobile while neither interacting with their nymphs nor expressing self-grooming, and as the total amount of time a mother did not move or interact with herself or her nymphs. In these videos, we also measured the total duration of mother-nymph interactions, defined as the sum of the total duration of allo-grooming (i.e., when the mother touches/scratches the body of a nymph with her mouthparts) and the total duration of stomodeal trophallaxis (i.e. mouth-to-mouth contacts between the mother and a nymph). We analyzed these movies using the software Boris v7.13.3 (Friard and Gamba 2016). In one movie (Cd concentration: 50mg.L⁻¹), mother-nymph interactions could not be analyzed due to a technical problem.

We quantified the level of feces production on day 10 after hatching, as a proxy of earwigs' digestive activity (Arcila and Meunier 2020; Van Meyel et al. 2021a, b). To do that, we isolated each mother on a humid filter paper in a Petri dish (9 cm diameter, 2 cm height) for 24h. After that time, we counted the number of feces pellets present on the ground.

Finally, we measured the relative weight change of each mother during the period of parent-offspring interactions on day fourteen after hatching. We defined this change as the difference in fresh weights between day 14 and day 1 after egg hatching divided by the fresh weight measured on day 1 after hatching. We also followed the survival of mothers by checking their survival daily.

Measurements of nymph development and survival

We also measured offspring development and survival rate during the period of parent-offspring interactions. We measured offspring development by their average weight change, which we calculated as the difference in mean fresh weight of nymphs between day 14 and day 1 divided by the mean fresh weight on day 1. We measured the survival rate of nymphs during parent-offspring interactions by counting how many of the 10 nymphs were still alive on day 14.

Statistical analyses

We conducted all statistical analyses using the software R v4.1.2 (www.r-project.org/). We analyzed nymph defense, self-grooming, inactivity, exploration, distance walked, pellet consumption, feces production, relative weight change of mothers and nymphs using a series of nine linear models (*lm* function of the package *car*; (Fox and Weisberg 2018), in which each variable was entered as a response variable. Because a large number of mothers did not express allo-grooming behavior, we tested whether cadmium concentration affected whether mothers showed allo-grooming or not (binomial response variable: 1 or 0, respectively) using a generalized linear model (*glm* function of the package *car*; (Fox and Weisberg 2018) fitted with a binomial distribution corrected for overdispersion. We analyzed the rate of nymph survival using another GLM fitted with a binomial distribution corrected for overdispersion. Finally, we analyzed the duration of nymph antennation using a GLM with a Poisson distribution corrected for overdispersion. In each of the statistical models, we entered the cadmium concentration as a categorical explanatory factor (five levels). We first added the maternal weight change and its interaction with cadmium concentration in each model, and then removed both as they never reached significance (their inclusion does not qualitatively change our results). We checked all model residuals for homoscedasticity, normal distribution and overdispersion (*check_model* and *check_overdispersion* functions of the *performance* package; (Lüdecke et al. 2020) and transformed the response variable where required. Correspondingly, we log-transformed the nymph defense, the distance walked, the food consumption, the feces production, the relative weight gain of nymphs, the durations of inactivity and exploration. When necessary, we conducted pairwise comparisons using estimated marginal means of the models and with *p* values corrected for multiple testing using Tukey methods (*emmeans* package).

The analyzed dataset included 102 of the 108 mothers initially set up in the experiment (*n* = 21, 19, 19, 22 and 21 families at 0, 12.5, 25, 50 and 100mg.L⁻¹, respectively). We had to exclude six mothers because three of them (2.8%) produced less than ten nymphs (one mother at 0mg.L⁻¹ and two mothers at 25mg.L⁻¹) and the three others (2.8%) died during the experiment (one mother per treatment at 12.5, 50 and 100mg.L⁻¹).

Results

Post-hatching maternal care and investment in care

Cadmium ingestion by mothers and nymphs did neither affect the expression of allo-grooming by mothers (fig 1A; LR $\chi^2_{(4)} = 8.88$, *P* = 0.064), nor the duration of mother-offspring antennations (fig 1B; LR $\chi^2_{(4)} = 0.37$, *P* = 0.985) or the relative weight change of mothers during the period of parent-offspring interactions ($F_{4,97} = 0.50$, *P* = 0.734). It only marginally affected the level of maternal defence against a simulated predator attack (fig 1C, $F_{4,97} = 12.86$, *P* = 0.037), as the number of pokes necessary to deter a mother was slightly higher for 100mg.L⁻¹ compared to 0mg.L⁻¹ (*t* = -2.74, *df* = 97, *P* = 0.054), while all other comparisons were not significant.

Noncare behaviours of mothers

The ingestion of cadmium by mothers affected the duration of self-grooming expressed by a female (fig 2A, $F_{4,96} = 3.29$, *P* = 0.014): mothers who ingested cadmium at 100mg.L⁻¹ spent more time self-grooming compared to a dose of 0mg.L⁻¹ (post-hoc test: *t* = -3.38, *df* = 96, *P* =

0.009), while the other values were intermediate (all other comparisons were non-significant). By contrast, cadmium ingestion did neither affect the duration of females' inactivity (fig 2B, $F_{4,96} = 0.52$, $P = 0.717$), nor the duration of females' exploration (fig 2C, $F_{4,96} = 0.31$, $P = 0.868$) or the distance walked by mothers (fig 2D, $F_{4,97} = 1.13$, $P = 0.347$). Moreover, it did not affect the two measured proxies of foraging activity, i.e. the amount of food consumed (fig 2E, $F_{4,97} = 0.15$, $P = 0.961$) and the number of feces pellets produced (fig 2F, $F_{4,97} = 0.32$, $P = 0.860$).

Nymph's development and survival

Cadmium ingestion by mothers and nymphs did not affect the survival rate of nymphs from hatching to the end of parent-offspring interactions (fig 3A, LR $\chi^2_{(4)} = 5.51$, $P = 0.239$). It also had no effect on the relative weight gain of the nymphs during this period (fig 3B, $F_{4,97} = 0.23$, $P = 0.921$).

Discussion

Cadmium is a highly toxic and diffusible element in the environment that is known to affect the survival, reproduction and physiology of many species (e.g. Cervera et al. 2004; Malakar et al. 2009; Li et al. 2018; Luo et al. 2020; Honorio et al. 2021). However, our study reveals that cadmium ingestion by earwig mothers and juveniles has only limited effects on the expression of maternal care, non-care behaviours and other life-history traits measured during the 14 days of parent-offspring interactions. Cadmium ingestion affected the level of females' selfgrooming, which was higher only in mothers fed with the highest dose of cadmium compared to those fed no cadmium. By contrast, the consumption of food contaminated with up to 100mg.L^{-1} cadmium did not alter the expression of post-hatching maternal care in terms of allo-grooming, antennal contact with nymphs and, to some extent, predator defence, as well as maternal investment in care (maternal weight change during parent-offspring interactions). It also did not affect maternal exploration, inactivity, distance walked, food consumption, feces production and survival, or nymph survival and relative weight gain during parent-offspring interactions.

Our data first show that the consumption of food contaminated with the highest dose of cadmium increased the time spent on self-grooming compared to cadmium-free food. In insects (including earwigs), self-grooming is often considered an adaptive and critical behaviour, which helps individuals to remove particles from their body surface (e.g. external pathogens and parasites, dirt; Boos et al. 2014) and apply self-secreted substances involved in desiccation resistance and/or chemical communication between conspecifics (Blomquist and Bagnères 2010; Wong et al. 2014). However, these functions are unlikely to explain our results as the earwig females ingested the cadmium and therefore had no apparent need to remove it from their cuticle. In vertebrates, self-grooming has the same function as reported in insects, but it may also be a non-adaptive behaviour resulting from anxiety and distress (Estanislau et al. 2019). In rodents, for example, the expression of repetitive and stereotyped expressions of self-grooming can be induced by exposure to different types of stress (e.g. predators or novel environments), regardless of the cleanliness of the environment and skin (Estanislau et al. 2013; Estanislau et al. 2019). Similarly, this over-expression is constitutive of several rodent models of neuropsychiatric disorders (Kalueff et al. 2016; H. Liu et al.

2021). To the best of our knowledge, this stress response has not been reported in insects (but see Root-Bernstein 2010; Zhukovskaya et al. 2013) but is a likely explanation for our results. This is also consistent with a previous study showing an increase in self-grooming in response to topical pesticide exposure, although we cannot exclude that in this study self-grooming was involved in removing pesticide particles from the cuticle (Meunier et al. 2020). If this hypothesis is true, then our results would also suggest that higher levels of stress do not alter the expression of post-hatch maternal care in earwigs, which could improve our understanding of the evolutionary drivers of the maternal care in this species. Future studies are nevertheless needed to confirm that self-grooming may be a non-adaptive response to stress in this species.

Apart from self-grooming, our data shows that cadmium consumption did not affect any other trait measured in mothers and juveniles during the 14 days following egg hatching. This is surprising because cadmium intake typically has negative effects on a wide range of traits, from survival to reproduction and development, in taxa from insects to mammals (Arito et al. 1981; Cervera et al. 2004; Malakar et al. 2009; Li et al. 2018; Jacquier et al. 2020 Sep 30; Luo et al. 2020; Honorio et al. 2021; Nanda and Firdaus 2022). Even more surprising, developing nymphs did not suffer increased mortality following cadmium ingestion. In many insects, early developmental stages are generally more sensitive to harmful chemicals than adults (e.g. with deltamethrin; Bouvier et al. 2002; Germano and Picollo 2018; Malbert-Colas et al. 2020). It could be expected that the development or survival of nymphs exposed directly to cadmium by ingestion would be affected. Moreover, these studies show that cadmium concentrations much lower than those used in our experiment can be sufficient to change behaviour. For instance, ingestion of $0.2\text{mg}\cdot\text{kg}^{-1}$ of cadmium affects reproductive behavior in the beet armyworm *Spodoptera exigua* (Su et al. 2021) and ingestion of $7\text{mg}\cdot\text{kg}^{-1}$ of cadmium impairs exploratory behavior in rats (Dési et al. 1998). Importantly, a previous study showed that individuals fed with cadmium (equivalent to $20\text{mg}\cdot\text{kg}^{-1}$) for three weeks accumulated this compound in their bodies (Honorio et al. 2023). Taken together, these results thus suggest that the earwig we tested did ingest cadmium, but that it had a limited effect on parent-offspring interactions and the outcome of group living. They also suggest that earwig mothers and nymphs have developed mechanisms of cadmium tolerance, resistance and/or detoxification that now deserve to be studied. In honeybees, for instance, cadmium exposure alters the microbiome and some bacterial strains can bioaccumulate this pollutant, making bees more resilient to cadmium (Rothman et al. 2019). Investigating the microbiome composition (Van Meyel, Devers, Dupont, et al. 2021) and its putative role in earwig cadmium resistance would be of great value.

Although our experimental design does not allow us to disentangle the effects of cadmium ingestion by mothers and nymphs on maternal care, it is unlikely that the apparent lack of effect reflects the sum of an increased need for care by contaminated nymphs and a reduced expression of care by contaminated mothers (i.e. that these two effects cancel each other). This is mainly because *F. auricularia* mothers typically reduce their expression of care towards juveniles that are in a poor physiological condition, e.g. due to starvation (Mas et al. 2009; Mas and Kölliker 2011). If the ingestion of cadmium by nymphs reduces their overall condition and thus increases their need for maternal care, then earwig mothers are likely to reduce rather than increase their expression of care. This, combined with the (expected) negative effects of maternal physiological deterioration on the expression of care, should lead to an overall reduction in maternal care. However, this is not what we have observed.

The results of this study, together with those of Honorio et al. (2023), show no effect of cadmium consumption (even at high doses) on the expression of maternal care and maternal investment in care both before and after hatching, on maternal expression of most non-care behaviours (except self-grooming), on mother survival, and on offspring survival and development in the European earwig. This surprising resistance to such a common and toxic pollutant raises important questions about the physiological mechanisms underlying the apparent lack of effect in earwigs (Karouna-Renier and Zehr 2003; Chen et al. 2016; Rothman et al. 2019; K. Liu et al. 2021), and its implications for their population dynamics and ecosystem functioning in contaminated environments. It also raises questions about the long-term effects of cadmium ingestion on reproduction and the behaviour of newly emerging adults, which should be investigated in future work.

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Author contributions

RH designed the study, reared earwigs, performed the experiment and statistical analyses, and wrote the manuscript. SM analysed videos, and contributed to the experiment and earwig rearing. CL designed the study, wrote the manuscript, and supervised the project. JM collected earwigs, designed the study, contributed to statistical analyses, wrote the manuscript, and supervised the project. All authors have read and approved the final version of the manuscript.

Data availability

Analyses reported in this article can be reproduced using the data and script provided by Romain Honorio (2023) (<https://zenodo.org/record/7662295>).

Compliance with ethical standards

Conflict of interest

The authors declare they have no conflict of interest.

Ethical note

No animal ethics approval was required. All individuals were handled with care.

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Figure legends

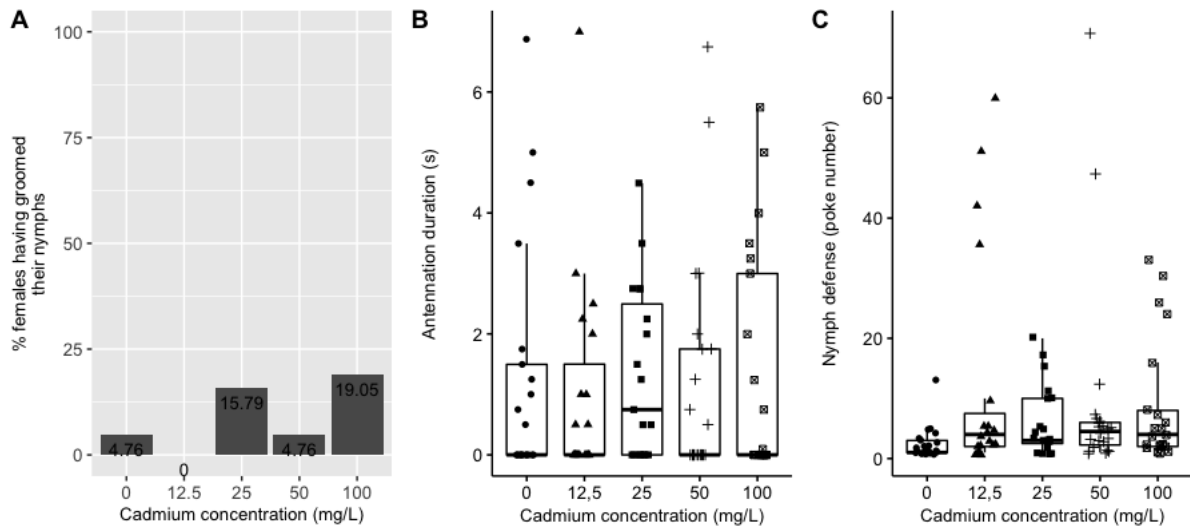


Figure 1: Effects of cadmium ingestion on three forms of maternal nymph care: (A) the expression of allo-grooming, B) the duration of nymph antenation, and C) the number of simulated predator attacks required to drive the female away. Boxplots depict the median (bold bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. For pairwise comparisons, different letters correspond to $P < 0.05$. The absence of letters on a figure indicates an absence of significant differences between all the tested doses.

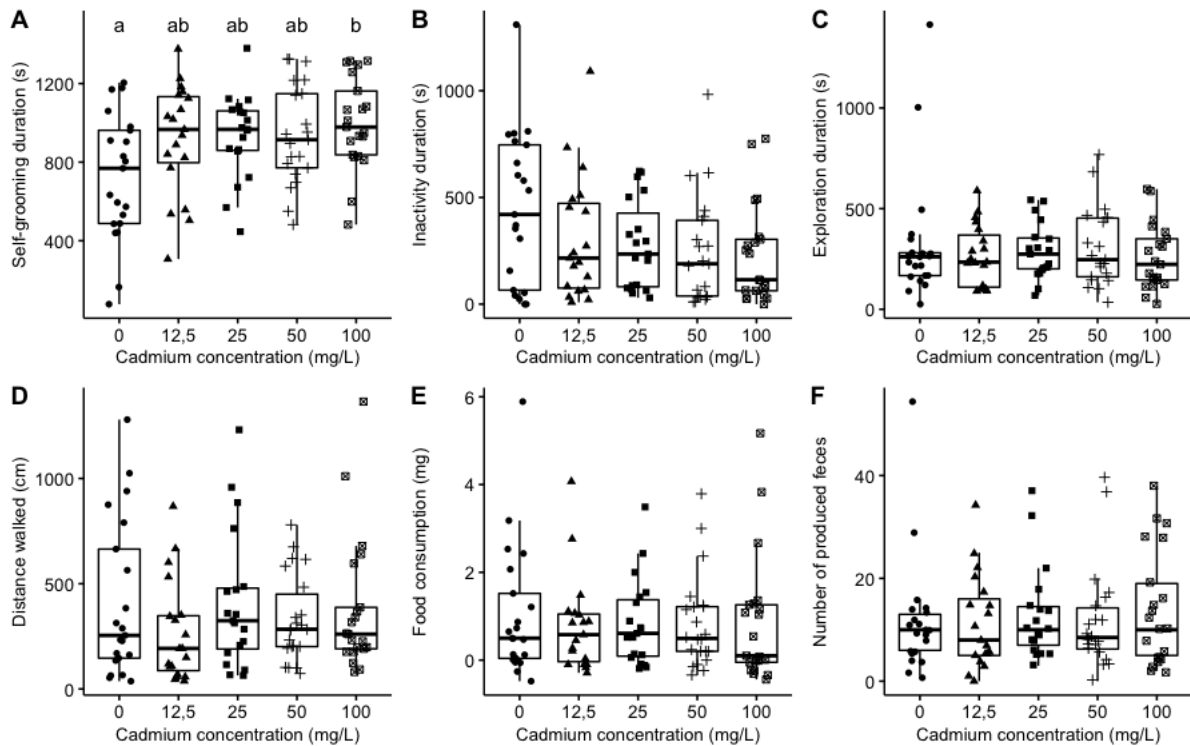


Figure 2: Effects of cadmium ingestion on the total duration of A) self-grooming B) inactivity and C) exploration expressed by mothers; D) the distance walked by mothers E) the amount of pollen pellet consumed and finally F) the number of feces produced. Boxplots depict the median (bold bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. For pairwise comparisons, different letters correspond to $P < 0.05$. The absence of letters on a figure indicates an absence of significant differences between all the tested doses.

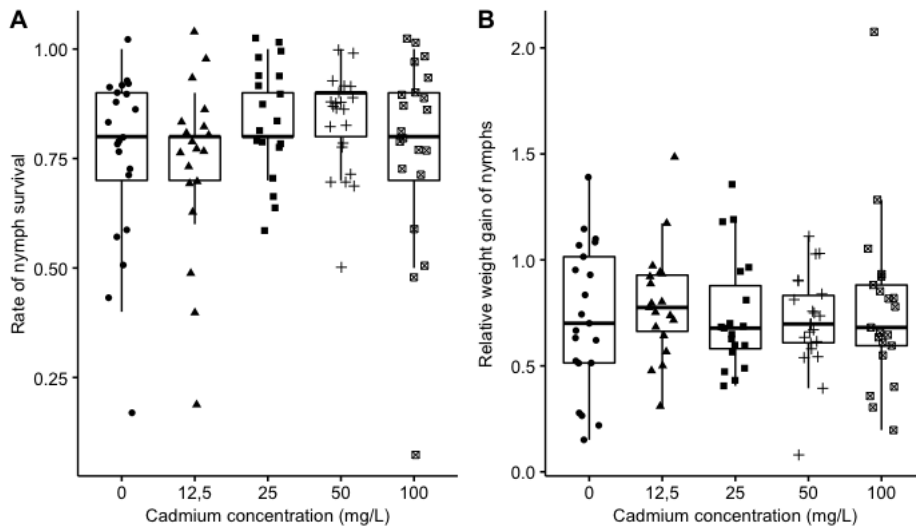


Figure 3: Effects of cadmium ingestion on A) the rate of nymph survival and B) the relative weight gain of nymphs during parent-offspring interactions. A value of '0' corresponds to no weight gained. Boxplots depict the median (bold bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. We did not detect any effect of cadmium concentration on the measurements presented in this figure

