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Effects of cadmium ingestion on reproduction and maternal egg care in the European earwig

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Abstract

A growing number of studies show that anthropization can alter the behavior, survival, physiology, cognition, and reproduction of many animal species. However, its impact on parental care, a common behavior where even subtle changes can have dramatic effects on the viability of future generations and thereby jeopardise population dynamics, remains surprisingly unclear. Here, we studied the effects of exposure to cadmium, a highly toxic chemical pollutant widely distributed in the trophic chain, on egg production and maternal egg care in the European earwig. We fed 200 females with food containing cadmium at five different concentrations for several weeks, and then quantified the number of eggs produced, the expression of six forms of egg care and three forms of non-care behaviors, as well as maternal survival and egg development. In contrast to most results reported in other animal species, we found no evidence that ingestion of even substantial doses of cadmium affects egg production and maternal egg care in the form of grooming, antennation, displacement, gathering, defense or retrieval. Moreover, it neither affected maternal exploration, inactivity and self-grooming behaviors, nor egg development time, hatching rate or juvenile weight. Overall, these results reveal that egg care is resilient to environmental cadmium pollution in earwigs, and suggest that females possess efficient and fast-acting physiological processes that help them reduce their sensitivity to heavy metal contamination. More generally, our findings may suggest that selection pressures associated with the necessity to express egg care has directly or indirectly selected for higher resistance/tolerance against certain chemical pollutions, and thus that species with parental care could be more resilient in the face of increasing levels of anthropogenic pollution.

Key-words: chemical pollutant, Dermaptera, *Forficula auricularia*, heavy metal, parental care, precocial species.

Introduction

Parental care is a taxonomically widespread phenomenon which typically confers substantial benefits to offspring (Meunier, Körner, & Kramer, 2022). Across oviparous species, it may occur before egg-laying in the form of nest building and egg provisioning, between egg-laying and egg hatching in the form of egg guarding and brooding, and after hatching in the form of brood attendance and food provisioning (Kramer & Meunier, 2019; Smiseth, Kölliker, & Royle, 2012). Pre-hatching parental care is often key to ensuring successful egg development as it protects eggs from environmental hazards (Smiseth et al., 2012). For example, egg care reduces egg desiccation in frogs (Delia, Ramírez-Bautista, & Summers, 2013), ensures a suitable temperature for egg development in shorebirds (AlRashidi et al., 2010), protects eggs against fungal infection in millipedes (Kudo, Akagi, Hiraoka, Tanabe, & Morimoto, 2011), and overall improves hatching success and quality of newly produced young in oviparous skinks (Lu, Wang, Kang, & Du, 2022). However, the diversity and breadth of benefits associated with egg care come with a substantial risk: impaired egg care can result in compromised embryo development and physiology, with negative long-term effects on the behavior, reproduction and survival of the offspring (Dettling, Feldon, & Pryce, 2002; Foster et al., 2012; Trumbo, 2013). Shedding light on the factors shaping the expression of egg care is thus crucial to improve our general understanding of the population dynamics of oviparous species (Cummings, Clemens, & Nunez, 2010; Fong-McMaster, Konji, Nitschke, & Konkle, 2020) and, more generally, of the evolutionary drivers of parental care.

Anthropogenic pollution is one of the main factors that can rapidly and pervasively change the expression of parental egg care in animals. Anthropization (e.g., urban expansion, landcover change, agriculture...) is steadily increasing around the world (Johnson & Munshi-South, 2017; Seto, Güneralp, & Hutyrá, 2012) and generally causes many types of pollution, be it light, noise, thermal, or chemical. Chemical pollution, in particular, is the subject of a growing body of research demonstrating effects on the behavior, cognition, and personality of numerous animal species (reviewed in Montiglio & Royauté, 2014; Scott & Sloman, 2004) at both the individual and the community level (Candolin & Wong, 2019). To date, the effects of chemical pollution on animal behavior have been mostly studied through the use of pesticides, for which even a single exposure to a sublethal dose can disrupt reproductive and foraging behaviors, hamper social organization (Fisher et al., 2021; Sloman et al., 2003), as well as impair the expression of certain forms of parental care as in rats, mice and several insects (Keller, Vandenberg, & Charlier, 2019; Meunier, Dufour, Van Meyel, Rault, & Lécureuil, 2020; Udo, Sandini, Reis, Bernardi, & Spinosa, 2014). However, it remains less clear whether long-term exposure to common chemical pollutants other than pesticides affects the expression of critical behaviors such as egg care, and thus whether exposure to these pollutants can have general effects on the evolutionary maintenance of parental care.

Heavy metals are a common source of chemical pollution worldwide and are present in both urban and non-urban areas (Foti et al., 2017; Liu et al., 2021). Among heavy metals, cadmium is particularly widespread, diffusive and toxic. Cadmium enters the environment through both anthropogenic activity (mining, fossil fuel combustion, traffic, farming...) and natural processes (volcano eruptions, forest fires, sea spray...), and can be found in both terrestrial (soil and groundwater) and aquatic environments (reviewed in Burger, 2008; Kubier, Wilkin, & Pichler, 2019). Cadmium generally accumulates in the food chain (Butt, Qurat-ul-Ain, Rehman, Khan, & Hesselberg, 2018; Munger, Hare, & Tessier, 1999; van Hattum et al., 1989) and can therefore be ingested by a wide range of species (if not all). The

consumption of this heavy metal entails many physiological and behavioral changes in various studied organisms. Physiological changes include, for instance, reduced growth in bluegills (Bryan, Atchison, & Sandheinrich, 1995), compromised growth and survival in grasshoppers (Malakar, Ganguly, & Haldar, 2009), and impaired growth, survival and fecundity in ants (Honorio, Jacquier, Doums, & Molet, 2021; Jacquier et al., 2020). Conversely, the behavioral changes include effects on cognition in humans (Gustin, Tofail, Vahter, & Kippler, 2018; Shao & Zhu, 2020), on locomotion and reproduction in *Drosophila* (Nanda & Firdaus, 2022), on aggressivity in rats (Arito, Sudo, & Suzuki, 1981) and on the formation of dominance hierarchies in trouts (Sloman et al., 2003). Considering the importance of egg care in the development and biology of many species (Meunier et al., 2022), it is surprising that the impact of cadmium on egg care remained unexplored until now.

The European earwig *Forficula auricularia* is an ideal insect to study the impact of cadmium on egg care. First, earwig females tend their clutch of eggs for about 40 days (Lamb, 1976; Ratz, Kramer, Veuille, & Meunier, 2016), during which they provide multiple, easily quantifiable forms of care such as aggressive protection against predators, egg cleaning to both remove fungal spores from eggshell and prevent eggs from desiccation, and frequent movement of the clutch to reach optimal development temperatures (Boos, Meunier, Pichon, & Kölliker, 2014; Diehl & Meunier, 2018; Tourneur, Cole, Vickruck, Dupont, & Meunier, 2022). These forms of care are essential, and eggs usually die within a few days if earwig mothers are removed from the clutch (Boos et al., 2014; Van Meyel, Devers, & Meunier, 2019). Changes to the expression of egg care can thus have dramatic effects on egg survival and population dynamics in this family-living species. Second, European earwigs are very likely to be exposed to bioaccumulated cadmium as they occur in many urban and agricultural systems worldwide, typically live under and above ground, and as omnivores consume organic matter from several trophic levels (Orpet, Crowder, & Jones, 2019). Finally, recent studies revealed that maternal egg care can be sensitive to chemical pollution in the form of pesticide exposure in this species: a single exposure to sublethal concentrations of a *Pyrethroid* pesticide (Deltamethrin) reduced the expression of maternal egg care (Meunier et al., 2020), while this effect was absent when exposed to an *Insect Growth Regulator* pesticide (Pyriproxyfen; Merleau et al., 2022).

Here, we fed each of 200 earwig females with food containing cadmium at one of five different concentrations for a minimum of three weeks before oviposition and then measured egg production, six forms of maternal egg care, and three forms of self-directed (non-care) behaviors. We also measured the survival of females during the period of egg care, and the outcome of egg care in terms of egg development time, hatching success and juvenile weight at egg hatching. Overall, we expected that the ingestion of (high concentrations of) cadmium would compromise the expression of maternal egg care and non-care behaviors, reduce female survival, and impair egg development and/or the quality of the resulting juveniles.

Material and methods

Biological model and rearing conditions

We used 200 *F. auricularia* females (species “A”; González-Miguéns et al., 2020; Wirth, Guellec, Vancassel, & Veuille, 1998) collected in July 2021 in peach orchards near Valence, France (Lat 44.9772790, Long 4.9286990). On the day of sampling, we transferred both females and males to large containers (32 x 20 x 16.5cm) to allow for uncontrolled mating

(Sandrin, Meunier, Raveh, Walser, & Kölliker, 2015). Back in the laboratory, we maintained these containers at 18-20°C under a 12:12h Light:Dark cycle, and provided the earwigs therein with an *ad libitum* amount of a standard diet food mainly composed of pollen, cat food, carrots, and agar (same composition as Kramer, Thesing, & Meunier, 2015) that was renewed twice a week. At the end of October 2021, we isolated each female in individual Petri dishes (5.5 cm diameter, 1.3 cm height) to mimic natural dispersal (Körner, Foitzik, & Meunier, 2018). These Petri dishes were furnished with moistened sand and maintained at 13°C under constant darkness to trigger egg production. We provided each isolated female with a standard amount of food (same composition as above, without Sorbic and Ascorbic acid) mixed with one of five quantities of cadmium (see details below). We then checked females every day to record the date of oviposition. Three days after oviposition, we counted the number of eggs produced (females typically lay all eggs within 3 days) and transferred each female and all of their eggs to a new Petri dish (5.5 cm diameter, 1.3 cm height) furnished with moistened sand. We did not provide food (and cadmium) to egg-tending females because earwig mothers typically stop their foraging activity during the period of egg care (Kölliker, 2007).

Cadmium exposure

To manipulate cadmium intake in the 200 tested females, we applied 10 µL of a cadmium solution directly to the standardized amount (50mg) of food provided to each female. We applied one of five concentrations of cadmium (0, 12.5, 25, 50 or 100 mg.L⁻¹), which were obtained by using pure MilliQ water or by diluting cadmium chloride powder (Sigma-Aldrich #202908) in MilliQ water, respectively. We renewed this mix (new food and new cadmium of the same concentration) twice a week for each female until egg production. At each change of food, we checked that at least part of it was consumed by the females, which was always the case. We used 40 females per concentration.

We have chosen this mode of exposure and the above-mentioned cadmium concentrations for three main reasons. First, food intake is the main source of cadmium exposure in nature (Genchi, Sinicropi, Lauria, Carocci, & Catalano, 2020; Munger et al., 1999; Zhang & Reynolds, 2019) so our method mimics natural cadmium ingestion by earwig females. Second, our concentration range includes the range of cadmium concentrations found in soil and in the food chain. In particular, cadmium concentrations range from 0.1 to 34 mg.kg⁻¹ in European soil (with most values between 1-10 mg.kg⁻¹; FitzGerald & Roth, 2015) and from 0.12 to 1.48 mg.kg⁻¹ in Asian soil (reviewed in Zhang & Reynolds, 2019), while cadmium concentrations can reach 1.95 mg.kg⁻¹ in the bivalve *Scapharca inaequivalvis* (Rangkadilok, Siripriwon, Nookabkaew, Suriyo, & Satayavivad, 2015; reviewed in Zhang & Reynolds, 2019), 5.8 mg.kg⁻¹ in the bird *Diomedea immutabilis* (Burger, 2008), 10 mg.kg⁻¹ in the carnivorous ladybird beetle *Coccinella septempunctata* and 48 mg.kg⁻¹ in the herbivorous insect *Ailopus thalassinus* (Butt et al., 2018). Finally, our concentration range covers the very few known non-aquatic examples where cadmium ingestion has impaired animal behavior. In particular, ingestion of 0.2 mgCd.kg⁻¹ affects reproductive behavior in the beet armyworm *Spodoptera exigua* (Su et al., 2021) and ingestion of 7 mgCd.kg⁻¹ impairs exploratory behavior in rats (Dési, Nagymajtényi, & Schulz, 1998).

To ensure that our manipulation of cadmium could affect egg production and egg care expression, we only included females that had ingested cadmium for at least three weeks

before oviposition in our analyses. Note that 0, 5, 4, 4 and 4 females from the 0, 12.5, 25, 50 and 100 mg.L⁻¹ treatments, respectively, produced eggs before this threshold and were excluded from further analyses after confirming that they were equally distributed across treatments ($\chi^2_{(4)} = 3.84$, $P = 0.428$). To confirm that this delay was long enough for earwigs to sequester cadmium, we conducted an additional experiment in which we measured the quantity of cadmium present in earwig males fed with cadmium for three weeks. In particular, we fed 10 males with a standardized amount of food on which we applied either a solution of cadmium (100 mg.L⁻¹; n = 5) or a solution of pure MilliQ water (Control; n = 5). The food was renewed twice a week, following the protocol described above. Three weeks later, we CO₂ anaesthetized the males for 2 min, froze them at -20°C, pooled them by cadmium concentration and finally mineralized the two pools of males with nitric acid (HNO₃, 68%) and hydrogen peroxide (30%). We then measured the quantity of cadmium in each pool using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES Agilent 5100SDVD, Agilent Technologies, Santa Clara, CA, USA) at the ALIPP6 platform (Sorbonne University), with a detection threshold of ICP-OES at 3µg.kg⁻¹. The results confirmed that three weeks were long enough to sequester cadmium, as we found 1740.2 µg of cadmium per kg of male in the pool of males fed with 100 mg.L⁻¹ of cadmium, compared to 4.0 µg of cadmium per kg of male in the pool of control males.

Measurements of female behavior and egg development success

We tested the effects of cadmium on six forms of egg care (egg antennation, egg grooming, egg displacement, egg gathering, maternal egg defense and delay of maternal return after clutch abandonment) and three non-care behaviors (self-grooming, exploration and inactivity) measured nine to eleven days after oviposition. We used the 125 females (n = 26, 25, 25, 25 and 24 mothers from 0, 12.5, 25, 50 and 100 mg.L⁻¹, respectively) that produced eggs at least three weeks after the first cadmium manipulation. All these behavioral measurements followed standard protocols in the European earwig (Meunier et al., 2020; Thesing, Kramer, Koch, & Meunier, 2015; Van Meyel et al., 2019).

Nine days after oviposition, we measured the time spent by each mother on egg antennation, egg grooming and egg displacement, as well as on self-grooming, exploration and inactivity (Meunier et al., 2020; Van Meyel et al., 2019). To this end, we first isolated each mother for 15 min in a new Petri dish (diameter 5.5 cm) to increase their motivation to interact with the eggs (Van Meyel et al., 2019), then returned each mother to its original Petri dish and finally recorded their behavior during the subsequent 20 min (Camera: BASLER BCA 1300, Germany; Media Recorder v4.0, Noldus Information Systems, Netherland). We analyzed the resulting videos using the software Boris v7.13.3 (Friard & Gamba, 2016) in which we defined the total duration of egg antennation, egg displacement and egg grooming as the total amount of time each mother spent on antennating at least one egg without mandibular contact, on displacing eggs within or away from the clutch, and on cleaning eggs with their mandibles, respectively (Boos et al., 2014). We also defined the total duration of self-grooming, exploration, and inactivity as the total amount of time each female spent on cleaning herself with mandibles (a behavior often used to remove dirt or external parasites and to apply protective chemical substances on the cuticle; Weiß, Kramer, Holländer, & Meunier, 2014), on being mobile while neither interacting with their eggs nor expressing self-grooming and as the total amount of time each mother did not move or interact with themselves or their eggs, respectively. We recorded all movies under infrared light, as earwigs are nocturnal, and

analyzed them blindly regarding the treatment. Two movies could not be analyzed due to a technical problem.

Ten days after oviposition, we measured maternal egg gathering. We gently isolated each mother for a few seconds, carefully scattered their eggs within the original Petri dish, then returned the mother to the Petri dish and two hours later, recorded whether or not the mother had gathered all her eggs in one pile, i.e., whether all eggs were within one egg distance from each other (Meunier et al., 2020).

Eleven days after oviposition, we measured the maternal egg defense and the delay of maternal return after clutch abandonment (Thesing et al., 2015). Maternal egg defense reflects the mother's willingness to protect her eggs from a simulated predator attack, while the delay of maternal return represents the time after which the female returns to her clutch after being chased away by a simulated predator attack. To conduct these measurements, 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 (close to the clutch). We measured the delay of maternal return just after the end of the egg defense measurement by recording the time the female took to return to her clutch (Van Meyel et al., 2019). We decided to fix the maximum time of maternal return at 30 min. Beyond this delay, we indicated that the female took more than 30 min to return to her clutch. Note that only five females (one female 0 mg.L⁻¹, three females 12.5 mg.L⁻¹ and one female 25 mg.L⁻¹) did not return to their clutch within 30 min after being chased away. After this last behavioral measurement, we maintained females and eggs under the standard conditions described above and checked them daily until egg hatching.

Upon egg hatching, we calculated the egg development time as the number of days between oviposition and egg hatching. One day later, we finally counted the number of newly hatched nymphs (all eggs in a clutch typically hatch within a day) to infer the hatching rate and weighed a random group of 10 nymphs per clutch (or all nymphs if less than 10 were available) to the nearest 0.01 mg using a microbalance (OHAUS© Discovery DV215CD).

Statistical analyses

We conducted all statistical analyses using the software R v4.1.2 (<http://www.r-project.org/>). We analysed egg number, egg grooming, egg antennation, egg displacement, egg defense, self-grooming, inactivity, exploration, and egg development time using a series of eight linear models (*lm* function of the package *car*; Fox & Weisberg, 2018), in which each variable was entered as a response variable. Because a large number of females did not express egg displacement behavior, we analysed this variable using a two-steps approach: we first used a generalized linear model (*glm* function of the package *car*; Fox & Weisberg, 2018) fitted with a binomial distribution corrected for overdispersion to test whether cadmium concentration affected whether females showed egg displacement or not (binomial response variable: 1 or 0, respectively). In a second step, we then used a linear model to test whether cadmium concentration affected the total duration of egg displacement among females that had displaced their eggs. We analysed egg gathering (1 or 0) and hatching rate using two GLMs fitted with a binomial distribution corrected for overdispersion. The hatching rate was entered using the *cbind* function in R (number of nymphs at hatching, number of laid eggs minus number of nymphs at hatching). Finally, we analysed the delay of maternal return using a Cox

proportional hazard regression model (*coxph* function of the *survival* package; Therneau, 2015) allowing for censored data to account for females that did not return to their eggs at the end of the observation time (see data in the results). Note that this analysis assumes that the females' return delays have hazard functions that are proportional over time for the different concentrations. In each of the statistical models described above, we entered the cadmium concentration as a categorical explanatory factor (five levels). To control that our results were independent of the number of days from first cadmium ingestion until oviposition (which varied from 21 to 112 days, mean \pm SE = 56.7 days \pm 2.2), we first added this factor 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 and normal distribution (*check_model* function of the *performance* package; Lüdecke, Makowski, Waggoner, & Patil, 2020) and transformed the response variable where required (we log-transformed the duration of exploration, self-grooming, and egg displacement and the number of pokes during egg defense; we square root-transformed the duration of egg grooming, egg antennation and inactivity, and we used a power function [⁵] to transform the egg development time).

Ethical note

We used a total of 200 earwig females. No animal ethics approval was required. All individuals were handled with care.

Results

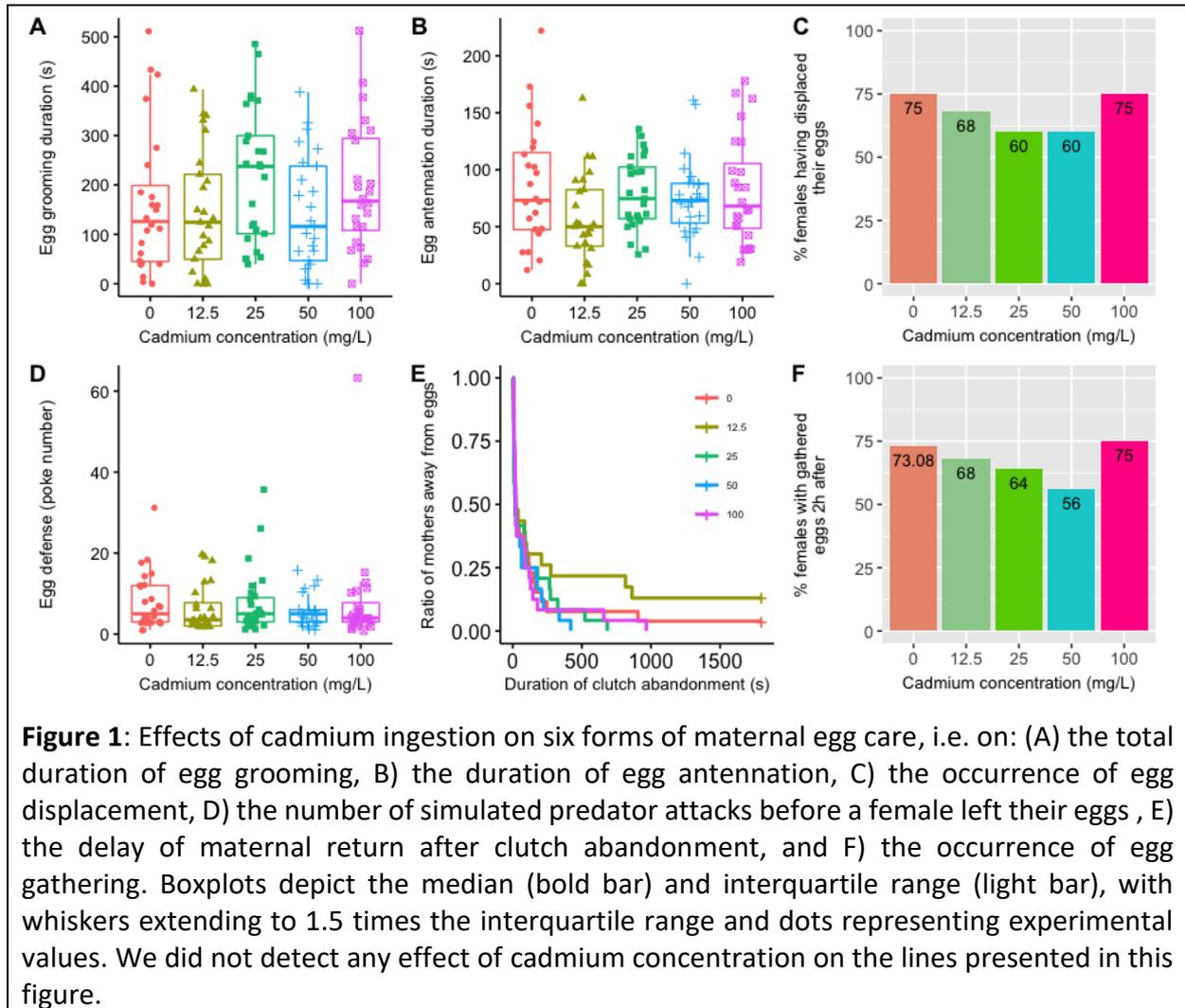
Overall, nine (4.5%) of the 200 tested females died during the experiment ($n = 3, 2, 2, 0$ and 2 females at 0, 12.5, 25, 50 and 100 mg.L⁻¹, respectively). These 9 females did not lay eggs before they died, and they were evenly distributed between the cadmium concentrations ($\chi^2_{(4)} = 2.61$, $P = 0.625$).

A total of 142 (71%) females laid eggs during the experiment ($n = 26, 30, 29, 29$ and 28 mothers at 0, 12.5, 25, 50 and 100 mg.L⁻¹, respectively) and this oviposition was independent of the cadmium concentration ($\chi^2_{(4)} = 0.56$, $P = 0.967$). Of these 142 females, 17 produced their clutch before reaching the three weeks of treatments and were thus excluded from the subsequent analyses. These provided us with measurements on 26, 25, 25, 25 and 24 females at 0, 12.5, 25, 50 and 100 mg.L⁻¹, respectively ($\chi^2_{(4)} = 0.08$, $P = 0.999$). Overall, these females produced 58.9 ± 1.2 eggs (mean \pm SE), a production that was independent of the doses of cadmium ingested before oviposition ($F_{4,120} = 1.10$, $P = 0.361$).

The six measured forms of maternal egg care were also independent of cadmium intake and concentration (Fig 1). Cadmium doses ranging from 0 to 100 mg.L⁻¹ did not affect egg grooming ($F_{4,118} = 1.96$, $P = 0.104$), egg antennation ($F_{4,118} = 2.24$, $P = 0.069$), the occurrence of egg displacement (LR $\chi^2_{(4)} = 2.43$, $P = 0.658$; and the total duration of egg displacement in females having displaced their eggs ($F_{4,78} = 2.28$, $P = 0.068$). Similarly, cadmium exposure did not affect egg gathering (LR $\chi^2_{(4)} = 2.49$, $P = 0.646$), egg defense ($F_{4,119} = 1.23$, $P = 0.790$) and the delay of maternal return after clutch abandonment ($\chi^2_{(4)} = 3.42$, $P = 0.490$).

Finally, the ingestion of cadmium by females prior to oviposition and at doses ranging from 0 to 100 mg.L⁻¹ neither had an effect on the expression of three non-care behaviors (Fig

2), nor on the outcome of egg care (Fig 3). In particular, it did not affect self-grooming ($F_{4,118} = 2.14, P = 0.080$), inactivity ($F_{4,118} = 0.43, P = 0.785$), and exploration ($F_{4,118} = 0.60, P = 0.664$; Fig 2), as well as egg development time ($F_{4,102} = 2.33, P = 0.061$), hatching rate ($\text{LR } \chi^2_{(4)} = 3.17, P = 0.529$) and mean nymph weight at hatching ($F_{4,100} = 0.15, P = 0.963$; Fig 3).



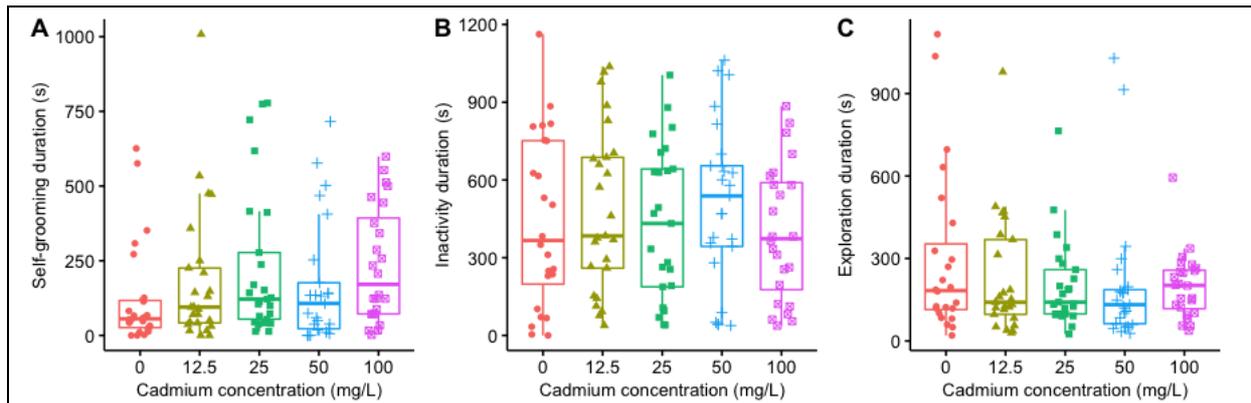


Figure 2: Effects of cadmium ingestion on the total duration of A) self-grooming B) inactivity and C) exploration expressed by mothers. Boxplots depict the median (bold bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. We did not detect any effect of cadmium concentration on the lines presented in this figure.

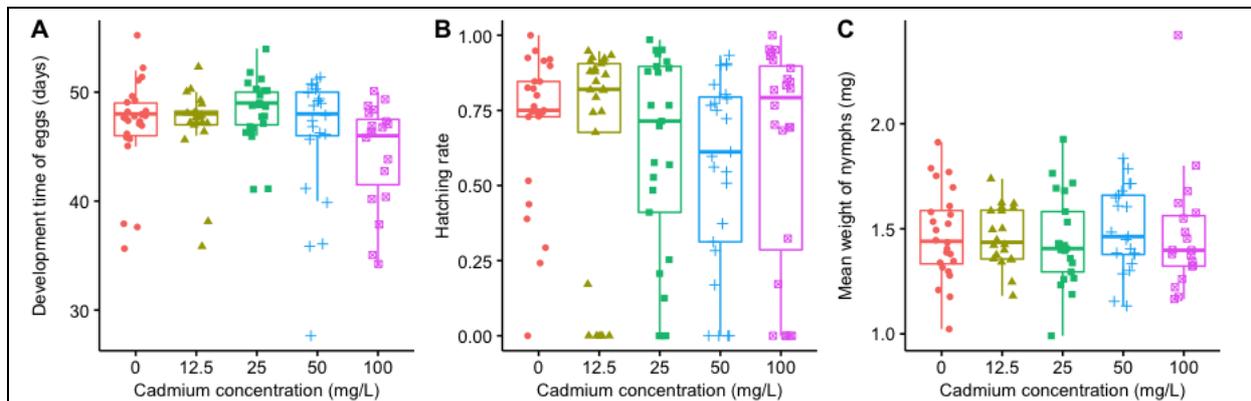


Figure 3: Effects of cadmium ingestion on the A) egg development time, B) egg hatching rate and C) nymph mean weight. Boxplots depict the median (bold bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. We did not detect any effect of cadmium concentration on the lines presented in this figure.

Discussion

Cadmium, a highly toxic and diffusible element in the environment, is commonly known to have negative effects on numerous life-history traits in animals, such as development, survival, immunity, fecundity and fertility (e.g. Bryan et al., 1995; Cervera et al., 2004; Honorio et al., 2021; Jacquier et al., 2020; Luo et al., 2020; Malakar et al., 2009; Nanda & Firdaus, 2022). In this study, we used the European earwig, to test, for the first time, its effects on egg production and maternal egg care - a major fitness-related social behavior occurring in a wide range of animals (Meunier et al., 2022). In contrast to most results reported in other animal species (see above), we found no evidence that cadmium ingestion impairs the behavioral or reproductive traits of earwig females. In particular, it had no effect on the expression of

maternal egg care in terms of egg grooming, egg antennation, egg displacement, egg defense, egg gathering and maternal return. Moreover, cadmium ingestion did not affect the expression of three maternal behaviors unrelated to egg care (exploration, inactivity and self-grooming), and did not impair five other major fitness-related traits, namely female survival, egg production, egg development time, hatching rate and nymph weight at hatching. These results are particularly striking as the tested females ingested realistic doses of cadmium for up to 112 days until they laid their eggs.

A first hypothesis to explain the apparent lack of effects of cadmium ingestion on egg care is that the expression of this behavior is so important for egg development that it does not depend on the mother's physiological state in earwigs. In birds and oviparous arthropods, egg care is indeed a key behavior that is often required to prevent full clutch failure (AlRashidi et al., 2010; Trumbo, 2013), and for which variation in the nature or intensity of expression can quickly have disastrous effects on the offspring. In line with this hypothesis, studies in fish and insects have shown that parents generally maintain the expression of care, even if this is accompanied by an increased risk of death. For instance, fathers face significant hypoxic stress to stay with their offspring and ensure viable offspring development in intertidal-nesting fish (Haupt et al., 2020), and pathogen-injected mothers maintain a high level of care despite high maternal mortality due to infection in the burying beetle *Nicrophorus vespilloides* (Ratz, Monteith, Vale, & Smiseth, 2021). Moreover, previous studies have shown that an absence of egg care typically leads to full clutch failure in the European earwig (Boos et al., 2014; Diehl & Meunier, 2018; Van Meyel et al., 2019). On the other hand, our data did not reveal any physiological costs associated with cadmium ingestion (such as reduced female survival, egg production or hatching rate), suggesting that earwig mothers did not sustain high levels of care by compromising their reproductive output or survival. Note that this was surprising, as our concentrations are close to the LC_{50} (i.e., doses leading to 50% mortality) of other insects such as 20 mg.kg^{-1} in the Asian corn larvae (Luo, Cao, et al., 2020) and 30 mg.kg^{-1} in the milkweed bug nymphs *Oncopeltus fasciatus* (Cervera et al., 2004) – even if LC_{50} can go up to $202\text{--}427 \text{ mg.kg}^{-1}$ in collembola adult *Orchesella cincta* (Posthuma, Verweij, Widianarko, & Zonneveld, 1993). Furthermore, previous studies have shown that a single exposure to a very low dose of other chemicals (pesticides) can impair earwig behaviors, including egg care (Malagnoux, Capowiez, & Rault, 2015; Meunier et al., 2020), indicating that this behavior may at least sometimes depend on the physiological state of earwig mothers.

An alternative, non-mutually exclusive, hypothesis to explain the apparent lack of effects of cadmium on egg care is that earwig females have physiological mechanisms that directly or indirectly help them reduce their sensitivity to heavy metal contamination. Cadmium is a highly toxic compound that has many adverse effects on metabolism, including changes of cell proliferation processes, DNA repair mechanisms and protein formation (inducing higher levels of oxidative stress in cells) (e.g. Martelli, Rousselet, Dycke, Bouron, & Moulis, 2006). Although our study does not allow to identify these mechanisms in earwigs, three could be at play: (i) the presence of enzymes that metabolize – and thereby free the organism from – toxic agents, (ii) the expression of stress-related genes when exposed to trace metals and/or (iii) the induction of specific changes in detoxification-linked turnover of proteins. These mechanisms have been reported in some animals such as *Daphnia pulex* and the collembola *Orchesella cincta*, which show a higher expression of metallothionein, a protein related with enhanced cadmium tolerance (Chen, Nichols, Poynton, & Sepúlveda, 2016; Roelofs et al., 2009); in the polychaete worm *Hediste diversicolor*, which has a higher

turnover of this protein (Mouneyrac et al., 2003); and in the midge larvae *Chironomus tentans*, which shows a higher expression of heat shock proteins (Karouna-Renier & Zehr, 2003) when facing heavy metal exposure. While these mechanisms could potentially reduce the costs of cadmium exposure below detectable levels and a recent study suggests that metallothioneins can be present in Dermaptera (Luo, Finet, Cong, Wei, & Chung, 2020), their presence in *F. auricularia* remains as yet unknown. Another strategy to reduce sensitivity to high levels of heavy metal contamination could be to sequester toxic agents in specific organs or separable body compartments. Specifically, contaminants could be sequestered in the cuticle, which is then removed by moulting as in collembola (van Straalen & van Wensem, 1986), or in the feces, as reported in larvae of the silkworm *Samia ricini* (Dutta, Kushwaha, Kalita, Devi, & Bhuyan, 2019), cotton leafworm *Prodenia litura* (Ding, Zhuang, Li, Xia, & Lu, 2013) and crustaceans (reviewed in Rainbow, 2007). Given the importance of feces exchange between adults and nymphs of the European earwig (Falk, Wong, Kölliker, & Meunier, 2014; Körner, Diehl, & Meunier, 2016; Van Meyel, Devers, & Meunier, 2021), cadmium detoxification via feces production would seem to be a poor strategy to get rid of toxic components in this species. Furthermore, our data show that cadmium is still present in males fed with a high dose for three weeks, suggesting that cadmium is not eliminated from (or metabolised by) their bodies. Future experiments are now needed to confirm that this apparent lack of elimination is not sex-specific in earwigs. Regardless of the mechanism reducing the sensitivity of earwigs to cadmium ingestion, our results suggest that it is very effective and rapid as it allowed even highly contaminated females to invest in survival, egg production and several behaviors at a normal rate, as well as prevented modifications in egg development, hatching rate and nymph weight at hatching. Hence, this calls for future studies identifying the physiological processes mediating the elimination, detoxification and/or metabolism of high doses of cadmium in this species, as well as testing whether parents can avoid cadmium-contaminated nesting areas and/or whether certain behaviours such as egg-grooming can help removing cadmium from the eggs (as earwigs already do against pathogens - Boos et al., 2014; Diehl & Meunier, 2018).

Notwithstanding the mechanisms responsible for the surprising lack of effects of high cadmium ingestion on egg production, egg care and survival in earwig females, our results raise fundamental questions on the nature and magnitude of the impact of anthropogenic pollution on the evolution of parental care in insects (and other animals). For instance, it suggests that selection pressures associated with the evolution of egg care may have directly or indirectly selected for physiological mechanisms that improve resistance to/tolerance against certain chemical pollutions. If this hypothesis holds true, this would suggest that species with parental care could be more resilient than previously thought in the face of environmental changes associated with increasing levels of anthropic pollution (e.g. species with egg-care are more likely to survive over a long-term in acidifying oceans; Lucey et al., 2015). This may be particularly true in Dermaptera where parental investment in parental care varies greatly both within and between species (Matzke & Klass, 2005; Wong, Meunier, & Kölliker, 2013). Such an hypothesis has been recently formulated for eusocial species, mostly based on the ability of their super-organismal colonies to keep homeostasis inside the nest/hive and to tolerate the loss of non-reproductive workers as long as the reproductive individuals are maintained (Parr & Bishop, 2022; Straub, Williams, Pettis, Fries, & Neumann, 2015). Here, our study suggests that other mechanisms could be at play in the absence of reproductive division of labor, and thus calls for more research investigating how the link

between parental care and resistance to anthropogenic pollution can impact the evolution of all forms of social life in a world facing global changes.

Declaration of interest

The authors declare they have no conflict of interest.

Author contributions

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

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Data availability

The dataset from this study is available on Zenodo ([10.5281/zenodo.7097309](https://zenodo.org/doi/10.5281/zenodo.7097309)).

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