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Sublethal exposure to deltamethrin stimulates reproduction and has limited effects on post-hatching maternal care in the European earwig

Emilie Mauduit, Charlotte Lécureuil*, Joël Meunier*

Institut de Recherche sur la Biologie de l’Insecte, UMR 7261, CNRS, University of Tours, Tours,
France

*Contributed equally to the work.

Corresponding authors: joel.meunier@univ-tours.fr; charlotte.lecureuil@univ-tours.fr

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ABSTRACT

Although pesticides are typically used to limit pest population, the diversity and nature of their unintentional effects on non-target organisms remain unclear. Better understanding these effects requires to carry out risk assessments on key physiological and behavioural processes specific to beneficial insects. In this study, we addressed this question by exposing mothers of the European earwig (a beneficial insect) to two sublethal doses of deltamethrin (a common pesticide in agriculture) during family life and measured the short- and long-term effects on a series of behavioural, physiological and reproductive traits. Somewhat surprisingly, our results first revealed that high and low doses of deltamethrin enhanced mothers' future reproduction by augmenting their likelihood to produce a second clutch, shortening the number of days until its production, and increasing the resulting number of eggs and their hatching rate. Conversely, the high dose of deltamethrin was detrimental, as it limited maternal brood defence, and reduced food consumption and expression of self-grooming. Finally, other traits were independent of deltamethrin exposure, such as three proxies of family interactions (i.e. distance to the brood, occurrence and duration of mother-offspring contacts), mothers' walking distance, and mother weight gain during family life. Our study overall demonstrates that sublethal exposure to a pesticide such as deltamethrin can have both positive and negative effects on non-target beneficial insects. It thus emphasizes that focusing on narrow parameters can lead to misleading conclusions about the unintended impacts of pesticides in treated agro-ecosystems and call for better considering this parameters diversity in integrated pest management programs.

INTRODUCTION

The sustainability of agricultural production has long been associated with the massive spraying of pesticides in fields and their surroundings (Aktar et al. 2009; Guedes et al. 2016). This is because large scale spraying often results in direct short-term benefits through acute mortality of pests and increased yields production (Torres and Bueno 2018). However, it is increasingly recognized that the presence of even low quantities of pesticides in the environment comes with unintended lethal and sublethal effects on a great diversity of non-target insects, among which many are of key agricultural, economic and ecological importance (Desneux et al. 2007; Royauté et al. 2015). Identifying the sublethal effects of pesticides, the temporality of their action, and the potential diversity of their impacts across non-target insects is therefore urgent to improve their use and prevent long-term or permanent damages to ecosystems.

Conducting risk assessment on the main physiological and behavioural processes specific to beneficial insects is a key method to better understand the unintended impacts of sublethal exposure to common pesticides such as deltamethrin (Dietz et al. 2009; Li et al. 2019). This molecule is a type II synthetic pyrethroid which - among other mechanisms - affects the sodium channel by prolonging the open phase of this channel in neurons (Narahashi et al, 1992). Its low toxicity to vertebrates, high efficacy against insects and low persistence in soil (Dietz et al. 2009; Li et al. 2019) have led to the common application of deltamethrin in many crops worldwide (e.g. apples, pears, peaches, sorghum, pineapple, coffee, and eucalyptus), as well as to its frequent use against mosquitoes, flies, cockroaches, and ticks (Davies et al. 2012; Liao et al. 2018). Despite its broad use in agriculture and the public health field, the sublethal effects of deltamethrin on non-target beneficial insects have been explored in a relatively

small number of species. In the honeybee, for instance, sublethal exposures to deltamethrin alter non-specific processes such as fecundity (Dai et al. 2010) and larval development (Yang et al. 2020) among other physiological and behavioural processes that are specifically important in this species, such as olfactory and learning capabilities (Decourtye et al. 2004), homing flight (Vandame et al. 1995), orientation and dancing communication (Thompson 2003; Zhang et al. 2020), and foraging activity and memory (Ramirez-Romero et al. 2005). Similarly, in several parasitoid wasps, deltamethrin impairs females' fecundity, larval development, but also behavioural processes such as sex pheromone discrimination, finding of the host location and walking (Salerno et al. 2002; Bayram et al. 2010; Delpuech et al. 2012; Delpuech and Delahaye 2013; Oliveira et al. 2018; Teder and Knapp 2019; Pereira Costa et al. 2020).

The European earwig *Forficula auricularia* is often considered a beneficial non-target Dermapteran insect frequently exposed to deltamethrin (note that it can also be considered as a pest because it causes damages in stone fruits; Orpet et al. 2019). This species is common in many agroecosystems worldwide, where it is an effective generalist predator of several pests such as aphids, leafrollers, and psyllids in pip-fruit orchards (Sauphanor and Sureau 1993; Colvin and Cranshaw 2010; Dib et al. 2010, 2011; Moerkens et al. 2011; Lordan et al. 2015; Orpet et al. 2019). The lethal and physiological effects of several pesticides commonly applied in crops and vineyards have been tested in earwig adults (Ffrench-Constant and Vickerman 1985; Colvin and Cranshaw 2010; Le Navenant et al. 2019; Orpet et al. 2019; Meunier et al. 2020). While these works report that many of these pesticides are toxic (Fountain and Harris 2015; Malagnoux et al. 2015b), they also show that exposures to normal application rates of deltamethrin have no impact on adults survival and predator activities (Malagnoux et al. 2015a; Meunier et al. 2020). Nevertheless, we recently demonstrated that

exposure to sublethal quantities of deltamethrin a few weeks before egg hatching subsequently impaired the expression of maternal egg care – a key behaviour in this species (Van Meyel et al. 2019), whereas it had no apparent effects on egg development and hatching success (Meunier et al. 2020).

In this study, we followed up on the results of Meunier *et al.* (2020) and investigated whether mothers' sublethal exposure to deltamethrin after egg hatching altered a series of specific and non-specific traits in terms of behaviours, physiology, and future reproduction. The behaviour and physiology of earwig females are indeed very different before and after egg hatching. While mothers stop their foraging activity and reduce their metabolism to focus on egg care during the 50 days preceding egg hatching (Koch and Meunier 2014; Van Meyel et al. 2019), post-hatching females exhibit an intense foraging activity, express multiple forms of care to their juveniles (called nymphs; Kölliker, 2007; Lamb, 1976; Vancassel and Foraste, 1980), as well as augment their metabolism and resume their vitellogenesis in anticipation of a (potential) second oviposition a few weeks later (Vancassel et al. 1984; Meunier et al. 2012; Körner et al. 2020; Tourneur and Meunier 2020). Moreover, this 14 days period of post-hatching family life is critical for earwig mothers, as it determines both the general quality of their adult descendants and the maternal timing of future reproduction (Kölliker 2007; Mas and Kölliker 2011a; Thesing et al. 2015; Kramer et al. 2017). Here, we exposed earwig mothers to two sublethal doses of deltamethrin or a control solution and subsequently measured 1) their activity, 2) level of food consumption, and 3) expression of self-grooming (an important behaviour in this species; Weiß et al., 2014). We also measured 4) the nature of mother-offspring interactions during family life in terms of distance to the brood, occurrence and duration of mother-offspring contacts, and maternal brood defence against a simulated predator attack, as well as 5) the level of maternal investment in future reproduction in terms

of likelihood to produce a second clutch, delay until 2nd clutch production, number of 2nd clutch eggs produced and hatching rate of these 2nd clutch eggs.

MATERIAL & METHODS

Animal sampling and rearing conditions

Our experiment involved a total of 106 *Forficula auricularia* L. females (and their nymphs produced under experimental conditions) field-sampled during the first week of July 2019 in a pip fruit orchard under Integrated Pest Management (IPM) and located in Pont-de-Ruan, France. Earwig adults were caught with wood traps previously placed on tree branches for one week. On the day of field-sampling, we transferred males and females in large plastic containers to allow uncontrolled mating (Sandrin et al. 2015). All the containers were then maintained under standard laboratory conditions, i.e. at 18 °C under a 12:12 h Light:Dark cycle (Meunier et al. 2012). Four months later, we discarded all males to mimic the life cycle of this species, and isolated each female in a Petri dish (90 mm diameter) lined with moistened sand and maintained at 10°C under constant darkness to trigger females' nest construction and oviposition (Körner et al. 2018). We checked each Petri dish every day to record the day of egg hatching. On the day following egg hatching, we counted the number of nymphs present in each of the 106 resulting families (mean \pm SE = 34.0 \pm 1.2 nymphs) and standardized it to 20 (min = 15; median = 20). We never mixed nymphs from different families. On that day, we transferred the Petri dishes to a climate chamber at 18°C and under a 12L/12D photoperiod cycle to allow nymph development (Meunier et al. 2012). From field sampling until the end of the experiment, we fed females twice a week with an *ad libitum* amount of a standard food mainly consisting of pollen, cat and bird food, wheat germ and agar (Kramer et al. 2015). Note

that females received no food from the day of oviposition to egg hatching, because females cease their foraging activity during this period (Kölliker 2007; Van Meyel and Meunier 2020).

Exposure to sublethal doses of deltamethrin

Six days after egg hatching (i.e. half the total duration of post-hatching family life; Meunier et al., 2012), we randomly exposed each mother to a deltamethrin or a control (absolute ethanol) solution using a standard protocol mimicking commercial sprayers and natural exposures to pesticides (Meunier et al. 2020). We used two concentrations of deltamethrin (68.750 and 6.875 ng/cm²) obtained by diluting the active deltamethrin molecule (Sigma-Aldrich #45423) in pure analytical grade ethanol (>99.5% absolute). These concentrations are non-lethal to earwig females (Meunier et al. 2020). They are respectively 4 times larger and 2.5 times smaller than the normal application rate (NAR) of commercial insecticide containing deltamethrin and allowed in French apple orchards (e.g. Decis Protech and Decis expert; Bayer©) that is 0.75 g/hl active ingredient equivalent to 17 ng/cm² (Malagnoux et al. 2015b). We conducted maternal exposures following a protocol established in Meunier *et al.* (2020), in which we directly applied 88 µL of either the deltamethrin (n = 36 for 68.750 ng/cm² and n = 36 for 6.875 ng/cm²) or the absolute ethanol (control; n = 34) solutions on the surface of a plastic Petri dish (diameter 35 mm). The Petri dish was then immediately and gently rotated to fully cover its ground and walls with the pesticide or control solution. The solution was subsequently allowed to evaporate for 30 min under an extractor hood. We then transferred each female to this Petri dish, where she could walk freely for 4h. At that time, we returned each mother to its original Petri dish (lined with wet sand) with a new standardized number of 15 nymphs (randomly taken from the 15 to 20 nymphs still alive at that time) to later conduct our behavioral and reproductive measurements (see details

below). The resulting families were maintained under standard conditions for the following 8 days, i.e. until the end of family life (Meunier et al. 2012). During the 4h of exposure, mothers were maintained under a constant artificial (white) light to stimulate their walking activity (the European earwig is a lucifugous species) and thus maximize contacts with molecules deposited on the Petri dish (Meunier et al. 2020).

Sublethal doses of pesticides typically induce no apparent mortality but potentially cause physiological and/or behavioural effects on individuals that survive the pesticides exposure (Desneux et al. 2007; Müller 2018). Here, we defined our two tested doses of deltamethrin as sublethal based on previous works showing that deltamethrin doses corresponding to normal application rates (NAR) in French apple orchards do not induce mortality in *F. auricularia* adults (Malagnoux et al. 2015a), and on our previous (and present) results demonstrating no excess of mortality with these two deltamethrin concentrations (Meunier et al. 2020).

Measurements during family life

We used the 106 mothers to successively test whether exposure to deltamethrin impacted maternal food consumption, brood care, activity, non-social behaviours, and weight change during family life. We first measured the level of maternal food consumption one hour after the end of the exposure, i.e. on day 6 after egg hatching. At that time, each mother was deposited in a Petri dish (diameter 35 mm) containing one pollen pellet that was previously weighed. Two hours later, we weighed the rests of the pollen pellet and returned each mother to its original Petri dish with nymphs. We defined the amount of pollen consumed by each mother as the difference between the two weight measurements. No mother has fully consumed its pellet. Because uncontrolled variation in air humidity can induce uncontrolled

variation in the fresh weight of pollen pellets, we added another control treatment (hereafter called “no mother treatment”; $n = 34$) in which we weighed pollen pellets maintained under the same conditions but without mothers.

We then measured the level of maternal brood defence on day 7 after hatching, i.e. 24h after female exposure. This form of post-hatching maternal care illustrates the females’ willingness to stand close to their brood to protect it from predator attacks (Lamb 1976; Ratz et al. 2016). Using a protocol established by Thesing *et al.* (2015), we counted the number of standardized simulated attacks (poking) that a female standing within one body length from its brood can endure before leaving the brood. Seven days after hatching, we transferred the Petri dish of each family to an experimental table and maintained them under red light for 15 minutes for acclimation. We then opened the lid and recorded where mothers were less than one body length away from the brood. These mothers were then standardly poked (one per second) on the pronotum with a glass capillary and we counted the number poke needed until they move more than one body length away from their initial position.

The activity of mothers was measured on day 8 after egg hatching, i.e. 48h after female exposure. On that day, we isolated each mother in a plastic apparatus consisting of two plastic arenas (4 cm diameter, 4 mm height) connected with a small corridor (2.5 mm) set up in between 2 glass sheets. The apparatus was immediately deposited on an infrared light table and then remained untouched for 15 minutes to allow acclimation to this novel environment. We then filmed mothers for 15 minutes (Camera: BASLER BCA 1300, Germany; Media Recorder v4.0, Noldus Information Systems, Netherland) and analyzed the resulting videos with the automatic tracking software ToxTrac v.2.90 (Rodriguez et al. 2018), with which we defined mothers activity as the total distance covered by each mother.

We measured the expression of mother-offspring interactions and mothers' non-social behaviours during family life (Mas and Kölliker 2011b; Weiß et al. 2014) on day 8 after egg hatching, right after the above-detailed measurements. At the end of the corresponding 15 min movies, we maintained each mother in the apparatus and carefully transferred its nymphs into the arena in front of it. We then filmed the resulting family life for 25 minutes. We first measured the total duration of mother-offspring interactions, defined as the sum of the total duration of allogrooming (i.e. the action of a mother touching/scratching the body of a nymph with its mandibles) and the total duration of stomodeal trophallaxis (i.e. mouth-to-mouth contacts between the mother and a nymph). We then measured the total duration of maternal self-grooming, defined as mothers touching/scratching a part of their own body with mandibles (Weiß et al. 2014). This is an important behaviour in earwigs, as it may help individuals to remove particles from the surface of their body (e.g. pathogens, dirt; Boos et al. 2014) and to apply self-secreted substances enhancing resistance against desiccation and communication between conspecifics (Blomquist and Bagnères 2010; Wong et al. 2014). The videos were analyzed with the software BORIS v.7.9.7 (Friard and Gamba 2016). All behavioural measurements (here and below) and video analyses were done under red light (earwigs are nocturnal) and blind regarding the type of female exposure.

Finally, we measured the weight change of mothers during the period of post-hatching family life. This change was defined as the difference of fresh weights between day 14 and day 1 after egg hatching (i.e. final minus initial fresh weights) divided by fresh weights measured on day 1 after egg hatching (i.e. initial fresh weight). Mothers were weighed to the nearest 0.01 mg with a microbalance (OHAUS® Discovery DV215CD).

Measurements of future reproduction

Fourteen days after egg hatching (i.e. at the end of post-hatching family life), a haphazard subset of 70 of the 106 experimental families (n = 22 for 68.750 ng/cm²; n = 24 for 6.875 ng/cm² and n = 24 for control treatments) was selected to test whether exposure to solvent or deltamethrin solutions altered (1) mothers' likelihood to produce a 2nd clutch, (2) the delay until 2nd clutch production, (3) the number of 2nd clutch eggs produced and (4) the hatching rate of these 2nd clutch eggs. The remaining 36 females were discarded from the experiment. On this day 14, nymphs were removed from every Petri dish to mimic natural family dispersion and allow newly isolated mothers to produce a second clutch (Meunier et al. 2012). These females were then maintained under constant darkness and received an *ad libitum* amount of the standard food, which was changed twice a week until the end of the experiment. The Petri dishes were checked daily to record the date of 2nd clutch oviposition and the date of egg hatching. Because eggs are generally laid within three days and hatch within one day (Koch and Meunier 2014), the number of 2nd clutch eggs was counted three days after the observation of the first egg and their hatching rate was calculated by dividing the number of 2nd clutch nymphs present one day after the observation of the first nymph by the number of 2nd clutch eggs produced. Females were considered as not producing 2nd clutch if no oviposition occurred during the 60 days following the 1st clutch production, as previous work indicated that females were very unlikely to produce a 2nd clutch more than 60 days after egg hatching (Meunier et al. 2012). Note that *F. auricularia* females typically produce up to 2 clutches in their entire lifetime, even if a few instances of a 3rd clutch production have been reported in a few North American populations (Tourneur 2018; Tourneur and Meunier 2020).

Statistics

All statistical analyses were performed with the software R v4.0.2 (<http://www.r-project.org/>) loaded with the packages *car*, *DHARMA* and *emmeans*. First, we conducted three generalized linear models (*glm* function in R) fitted with binomial error distribution, in which the response variable was either whether mothers were close to their brood at day 7 (after egg hatching), the occurrence of at least one contact with their nymphs at day 8, or mothers' likelihood to produce a 2nd clutch of eggs. In these three models, we used a *cloglog* link-function to correct for the unbalanced representation of 0 and 1 in the data sets. Then, we used eight general linear models (*lm* function in R), in which the response variable was either the amount of pollen pellet consumed by mothers at day 6, the number of pokes necessary to deter mothers from their brood at day 7, the walking distance of mothers at day 8, the duration of mother-offspring contacts at day 8, the self-grooming duration at day 8, the number of days between the end of family life and the day of 2nd clutch production, the number of 2nd clutch eggs or the hatching rate of these 2nd clutch eggs. In each of the 12 models detailed above, females' exposure (68.750 ng/cm² deltamethrin, 6.875 ng/cm² deltamethrin or evaporated ethanol) was entered as a categorical explanatory factor. In the model testing the amount of pollen pellet consumed by mothers, the explanatory factor also included an additional "no mother" level for the treatment without mothers. When required, pairwise comparisons between treatments were conducted using the estimated marginal means of the models, with p-values corrected for multiple testing using Tukey methods. We verified the normal distribution of the residuals and the homoscedasticity of each statistical model using the diagnostics tools available in the R package *DHARMA* (Hartig 2020). To fulfil the assumptions of the corresponding models, we had to log-transform the number of pokes necessary to deter mothers from their brood and the duration of mother-offspring contacts.

RESULTS

Overall, only 3 (3%) of the 106 tested mothers died during the experiment. These females were evenly distributed among the treatments, with one female (3%) involved in the control treatment, one (2.9%) in the high deltamethrin treatment (68.750 ng/cm²) and one (2.9%) in the low deltamethrin treatment (6.875 ng/cm²). These three females were excluded from the following statistical analyses.

Food consumption, activity, non-social behaviours, and weight change

Deltamethrin exposure altered the amount of pollen eaten by mothers on the day of exposure (Figure 1A; $F_{3,133} = 34.44$, $P < 0.0001$): this amount was lower in mothers exposed to high quantities of deltamethrin compared to mothers exposed to low quantities of deltamethrin (model contrasts; $t_{133} = 5.16$, $P < 0.0001$) and solvent (model contrasts; $t_{133} = 5.77$, $P < 0.0001$). By contrast, this amount was comparable between mothers exposed to low quantities of deltamethrin and solvent (model contrasts; $t_{133} = 0.68$, $P = 0.905$). Notably, the three types of mothers consumed pollen during the experiment, as we detected a larger weight loss in the pollen pellets from the treatments where the mothers were present (Solvent, low and high) compared to absent (model contrasts; No mother/Solvent : $t_{133} = -8.60$, $P < 0.0001$; No mother/low: $t_{133} = -8.04$, $P < 0.0001$; No mother/ high: $t_{133} = -2.91$, $P = 0.022$).

Deltamethrin influenced the total duration of maternal self-grooming (Figure 1B; $F_{2,100} = 4.18$, $P = 0.018$) : This total duration was shorter in mothers exposed to high quantities of deltamethrin compared to mothers exposed to solvent (model contrasts; $t_{100} = 2.69$, $P = 0.023$). This trend was conserved between high and low quantities of deltamethrin, but it was only close to a statistical significance (model contrasts; $t_{100} = 2.25$, $P = 0.068$). The total

duration of self-grooming was not significantly different between mothers exposed to low quantities of deltamethrin and solvent (model contrasts; $t_{100} = 0.47$, $P = 0.886$).

Finally, we did not detect an effect of deltamethrin exposure on mothers walking distance (Figure 1C; $F_{2,100} = 1.60$, $P = 0.208$). There was also no effect of deltamethrin on the proportion of weight gained by mothers during the period of family life, i.e. from day 1 to day 14 after egg hatching (Figure 1E; $F_{2,100} = 0.61$, $P = 0.544$).

Mother-offspring interactions

Deltamethrin exposure affected the level of maternal defence against a simulated predator attack (Figure 2A; $F_{2,79} = 5.61$, $P = 0.005$): the number of pokes necessary to deter a mother from its brood was lower in mothers exposed to high quantities of deltamethrin compared to mothers exposed to low quantities of deltamethrin (model contrasts; $t_{79} = 2.58$, $P = 0.015$) and solvent (model contrasts; $t_{79} = 3.03$, $P = 0.009$). By contrast, this number was comparable between mothers exposed to low quantities of deltamethrin and solvent (model contrasts; $t_{79} = 0.14$, $P = 0.990$). Moreover, we did not detect an effect of deltamethrin exposure on the likelihood of a mother to be close to its brood just before the poking experiment (Figure 2B; LR $\chi^2_2 = 5.75$, $P = 0.065$), on the occurrence of at least one contact between the mother and the brood (Figure 1C; LR $\chi^2_2 = 1.61$, $P = 0.447$) and on the total duration of these contacts when they occurred (Figure 2D; $F_{2,53} = 0.274$, $P = 0.762$).

Future reproduction

Deltamethrin exposure overall increased maternal investment into future reproduction in terms of likelihood to produce a 2nd clutch (Figure 3A; LR $\chi^2_2 = 6.76$, $P = 0.034$), days until 2nd clutch production (Figure 3B; $F_{2,46} = 5.20$, $P = 0.009$), number of 2nd clutch eggs (Figure 3C; $F_{2,44} = 4.59$, $P = 0.016$) and hatching rate of 2nd clutch eggs (Figure 3D; $F_{2,44} = 5.34$,

P = 0.008). First, the likelihood to produce a 2nd clutch was higher in females exposed to low quantities of deltamethrin compared to solvent (model contrasts; $Z = -2.55$, $P = 0.029$), while we did not detect significant differences in the other comparisons (Solvent vs High quantities: $Z = -1.20$, $P = 0.455$; High vs Low quantities: $Z = 1.34$, $P = 0.374$). Second, the delay until 2nd clutch production was shorter in mothers exposed to low and high quantities of deltamethrin compared to solvent (model contrasts; High quantity versus Solvent: $t_{46} = 3.13$, $P = 0.008$; Low quantity versus Solvent: $t_{46} = 2.43$, $P = 0.049$), with no difference between high and low quantities of deltamethrin ($t_{46} = -0.55$, $P = 0.847$). Third, the number of 2nd clutch eggs was larger in mothers exposed to both high and low quantities of deltamethrin compared to solvent (model contrasts; High versus Solvent: $t_{44} = -2.86$, $P = 0.017$; Low versus Solvent: $t_{44} = -2.46$, $P = 0.046$), with no difference between high and low quantities of deltamethrin ($t_{44} = -0.689$, $P = 0.766$). Finally, the hatching rate of 2nd clutch eggs was larger in mothers exposed to low quantities of deltamethrin compared to solvent (model contrast; $t_{44} = -3.27$, $P = 0.006$), whereas we did not detect significant differences between the other treatments (Solvent vs High quantities: $t_{44} = -1.98$, $P = 0.130$; High vs Low quantities: $t_{44} = 1.17$, $P = 0.475$).

DISCUSSION

A better understanding of the unintended effects of pesticides on agro-ecosystems requires risk assessments on specific and non-specific traits in non-target beneficial insects. In this study, we exposed earwig mothers to sublethal doses of deltamethrin (the active component of commercial insecticides allowed in French apple orchards) during post-hatching family life and measured the effects on a series of traits reflecting mother's investment in future reproduction, post-hatching care, self-grooming and activity. Somewhat surprisingly, our results first revealed that exposure to low quantities of deltamethrin (6.875 ng/cm²)

enhanced mothers' future reproduction by augmenting their likelihood to produce a 2nd clutch, shortening the number of days until 2nd clutch production, increasing the resulting number of 2nd clutch eggs and improving their hatching rate. These positive effects on female's reproduction were also present in mothers exposed to high quantities of deltamethrin (68.750 ng/cm²), even if two measurements (2nd clutch production and hatching rate) were non-statistically significant. Contrary to these effects, our results then show that exposure to high quantities of deltamethrin impaired brood defence against a predator attack, as well as reduced mothers' pollen consumption and expression of self-grooming. Finally, our data suggest that deltamethrin does not impact several other traits, including mothers activity in terms of walking distance, three other measurements of family interactions (i.e. distance to the brood, occurrence and duration of mother-offspring contacts), and mother weight gain during the period of family life.

Although counter-intuitive, the reported reproductive stimulation of earwig mothers exposed to deltamethrin is in line with previous works conducted in a few other pests and non-target insects exposed to sublethal quantities of pesticides (including deltamethrin; Azzam et al., 2009; Guedes et al., 2010; Lalouette et al., 2016; Yin et al., 2008). Because our exposure occurred 6 days after egg hatching - a period at which earwig females augment their metabolism and resume vitellogenesis (Vancassel et al. 1984; Meunier et al. 2012; Körner et al. 2020; Tourneur and Meunier 2020), we hypothesize that deltamethrin directly or indirectly acts on vitellogenesis in this insect, e.g. via oxidative stress or hormonal modification. However, the mechanisms at the origin of this effect remain to be investigated. Notwithstanding these mechanisms, the reported differences between low and high quantities of deltamethrin on reproduction suggest a hormetic effect, defined as an adaptative biphasic dose-response where low doses result in protective effects while high

doses result in detrimental effects (Cutler 2013; Berry III and López-Martínez 2020). Such hormetic effect of deltamethrin has been reported on other traits and in other insect species, such as on male responses to sex pheromone in the cotton leafworm *Spodoptera littoralis* (Lalouette et al. 2016; Malbert-Colas et al. 2020) and in the maize weevil *Sitophilus zeamais*, where higher grain consumption and increased progeny emergence were observed with low exposures (Vélez et al. 2018).

The reproductive stimulation induced by deltamethrin exposure was not associated with a higher food intake by the exposed mothers, a reduced the activity of these mothers or a reallocation of energy from the care of current brood to the production of future brood. In particular, deltamethrin exposure reduced pollen consumption, did not affect walking distance, and reduced one of the four measured proxies of maternal care (brood defence). Moreover, this latter effect occurred with the high dose of deltamethrin only, and the positive effects on future reproduction were the strongest with the low dose. Overall, these findings call for future works shedding light on the energetic origin of second clutch production, and the nature and strength of the potential costs associated with this reproductive stimulation. A potential cost could be a reduced lifespan (Kliot and Ghanim 2012), which we were not able to test in this study due to the extended earwigs' longevity (250 to 300 days; Tourneur and Meunier, 2020).

Our data report contrasting effects of deltamethrin exposure on post-hatching maternal care. Deltamethrin exposure reduced the level of brood defence against a predator attack but affected neither mother's proximity to its brood nor the occurrence and total duration of mother-offspring interactions. It has been recently proposed that investigating the sublethal effects of pesticides on the expression of parental care in non-target organisms

should be of particular interests. Indeed, the associated alterations in offspring's development, survival and reproductive success could shape the long-term efficiency of pesticide use, and the maintenance and population dynamics of a large number of these species (Cummings et al. 2010; Fong-Mcmaster et al. 2020). This prediction received supports from a handful of studies conducted in mice and rats showing, for instance, that mothers fed with organochlorine pesticides exhibit a lack of retrieval behaviour (Matsuura et al. 2005) and shorten their nursing behaviours (Palanza et al. 2002), while mothers exposed to a phosphonoglycine pesticide augment their licking behaviour towards pups (Dechartres et al. 2019). Our results reveal that exposure to sublethal doses of deltamethrin 6 days after egg hatching only has limited impact on the expression of post-hatching family life in earwigs. Given that post-hatching maternal care can have long-term effects on adults offspring in earwigs (Kölliker 2007; Mas and Kölliker 2011a; Meunier and Kölliker 2012; Thesing et al. 2015; Vogelweith et al. 2017; Kramer et al. 2017), future works should investigate whether and how (even subtle) pesticide-driven alterations in the expression of post-hatching maternal care shape juvenile's development, survival and reproductive success.

Interestingly, our findings reveal that the same sublethal quantities of deltamethrin trigger different effects when maternal exposure occurs after (this study) and before (Meunier et al. 2020) egg hatching. Our previous study indeed showed that mothers exposure about 35 days before egg hatching did not affect (compared to reduced) the number of pokes necessary to deter a mother from its clutch of eggs, increased (compared to decreased) maternal self-grooming, and impaired almost every (compared to only one) measured form of maternal care (i.e. egg gathering, egg grooming and clutch maintenance; Meunier et al., 2020). This overall suggests that the outcome and strength of sublethal effects of deltamethrin depend on the period of the life cycle at which mothers are exposed and/or on the measured traits, either

due to different regulatory pathways of maternal care towards eggs and nymphs or a changing role of these traits during earwigs' life cycle. For instance, self-grooming is an important non-social behaviour in insects (including earwigs), which is typically used to remove pathogens and other particles from the cuticle, and to apply self-secreted substances on the cuticle to improve protection against desiccation and allow communication between conspecifics (Blomquist and Bagnères 2010; Weiß et al. 2014; Małagocka et al. 2019). Because earwig mothers typically live alone in a closed nest before egg hatching (Lamb 1976), they could reduce their allocation into self-grooming at lower costs compared to post-hatching mothers, because they comparatively experience almost no variation in ambient humidity, no possibility of social interactions, and limited risks of encountering new pathogens.

To conclude, our study demonstrates that sublethal exposure to a pesticide such as deltamethrin can have both positive and negative effects on non-target beneficial insects. This emphasizes that focusing on a narrow set of parameters such as either standard behaviours (e.g. food consumption and activity), species-specific behaviours (e.g. maternal egg and post-hatching care in earwigs) or physiological parameters (e.g. weight gain and reproduction) can lead to misleading conclusions about the unintended impacts of pesticides in treated agroecosystems. More generally, our study stresses that studying the diversity of sublethal effects is essential to improve our general knowledge on pesticides use and on their potential risks in integrated pest management programs.

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Authors' contributions. EM, CL and JM: Conceptualization, Methodology and Validation. EM: Data acquisition. EM and JM: Statistical analysis. EM, CL and JM: Manuscript writing, reviewing and editing.

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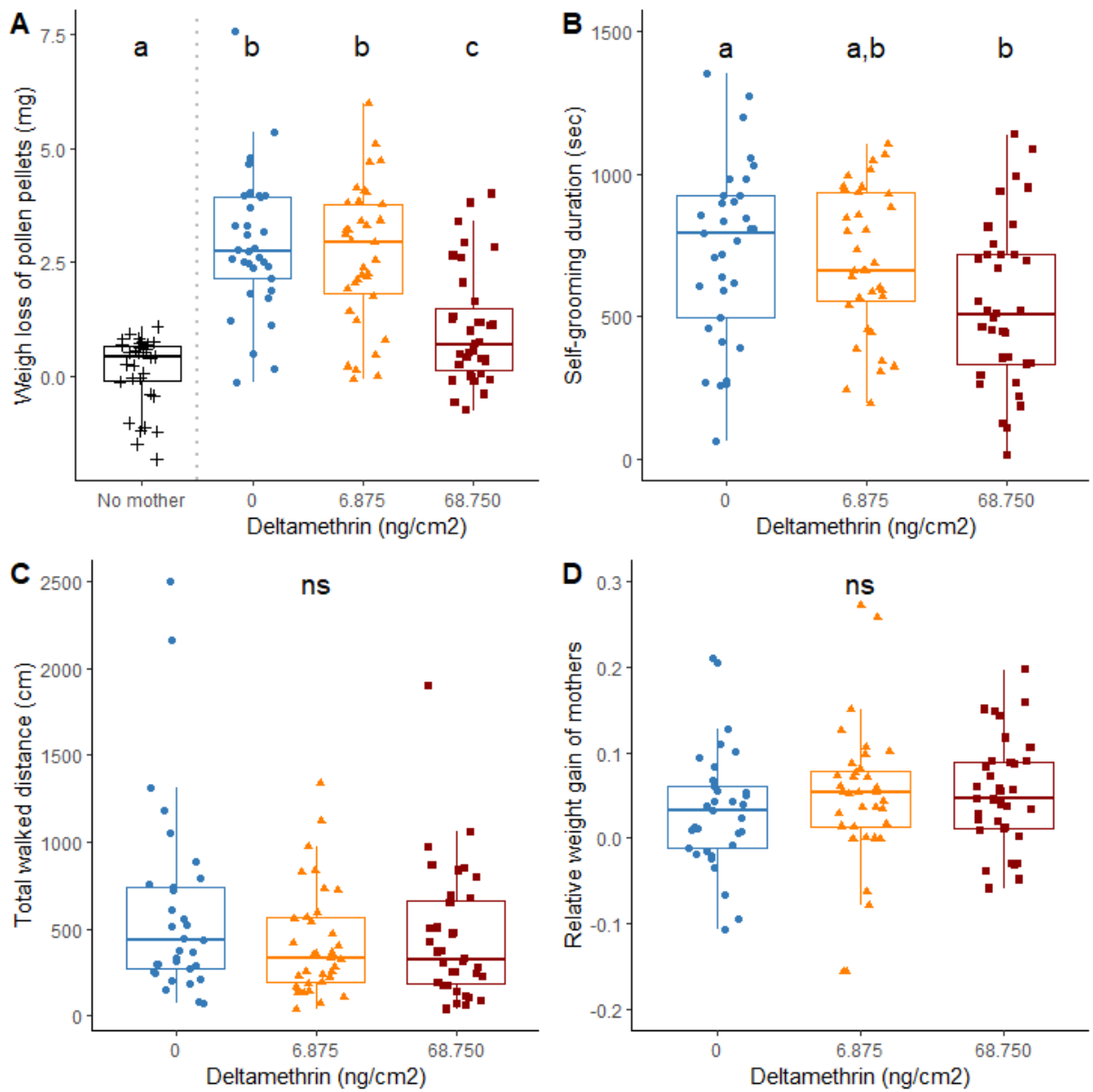


Figure 1. Effects of deltamethrin exposure on mothers' (A) pollen consumption, (B) expression of self-grooming during family life, (C) total walked distance, and (D) the relative fresh weight gained by mothers over the 14 days of family life. Box plots depict median (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. Different letters refer to $P < 0.05$, ns refers to $P > 0.05$.

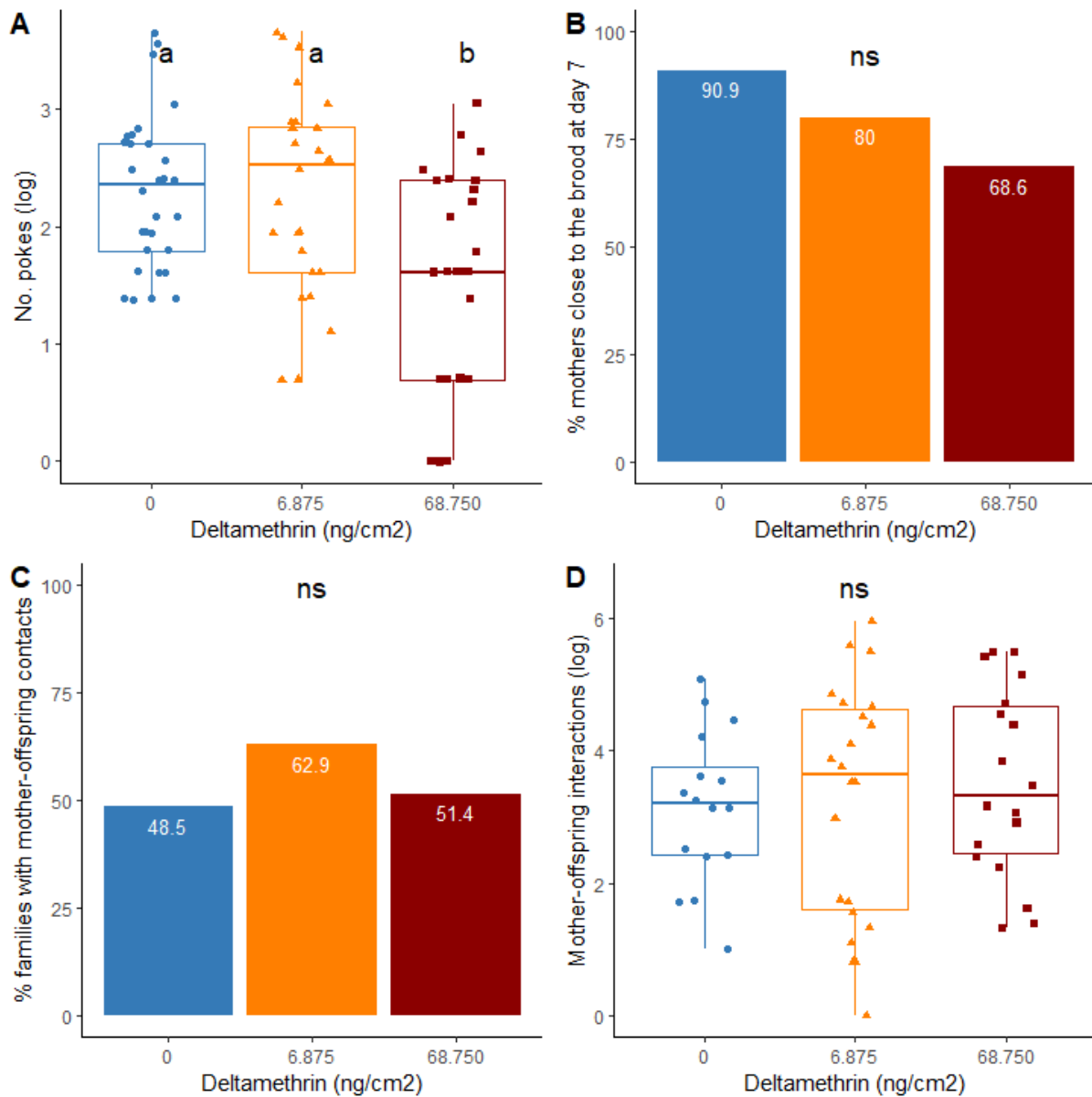


Figure 2. Effects of deltamethrin exposure on post-hatching maternal care and family interactions. (A) Number of pokes needed to deter mothers from their brood. (B) Proportion of mothers within one body length of their brood on day 7 after egg hatching. (C) Proportion of families in which mothers interacted with their brood at least once over 25 minutes of video recordings on day 8. (D) Total duration in seconds of mother-offspring interactions - when present - occurring over 25 minutes of video recordings on day 8. Box plots depict median (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. Different letters refer to $P < 0.05$, ns refers to $P > 0.05$.

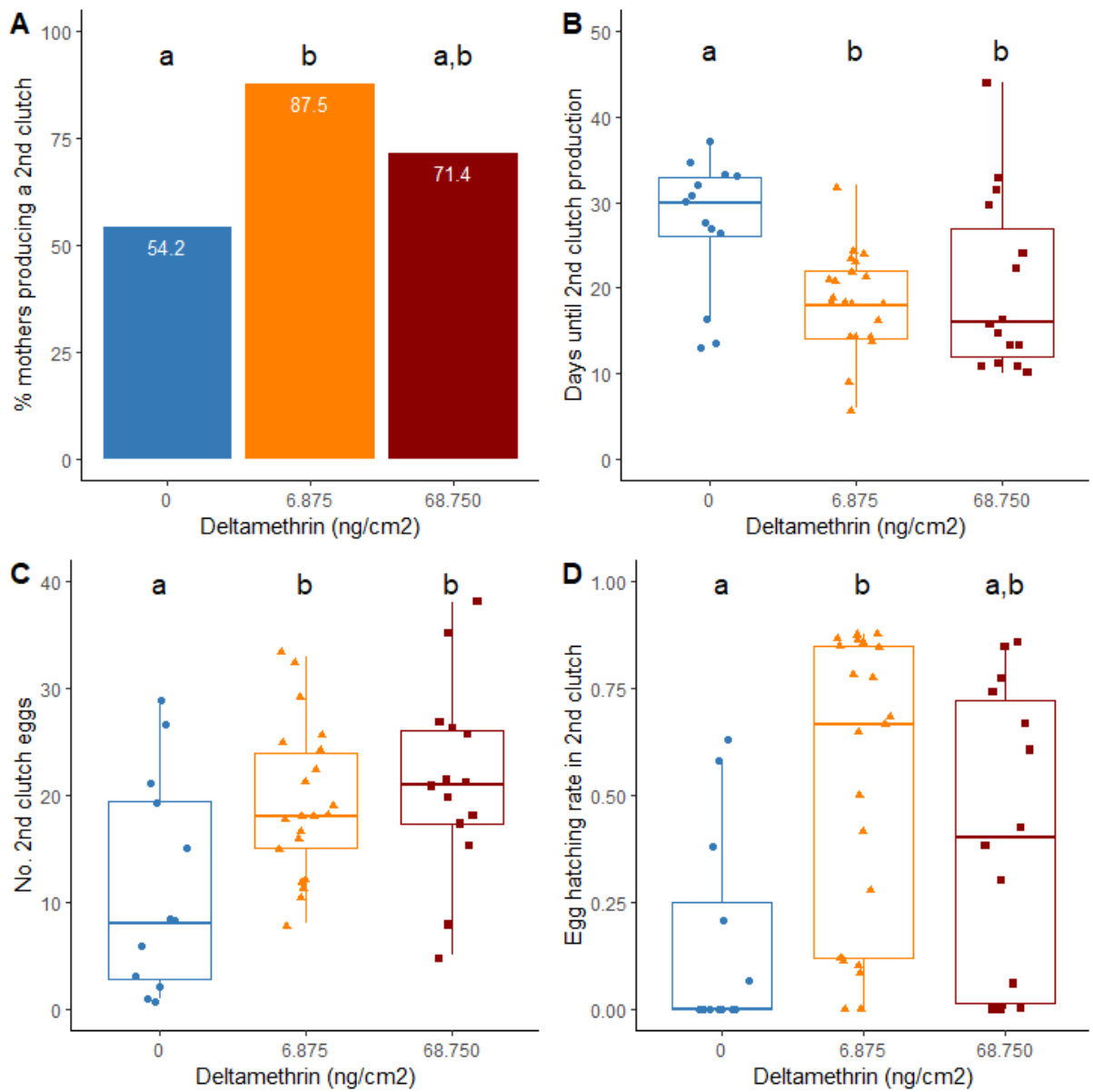


Figure 3. Effects of deltamethrin exposure on (A) mothers' likelihood to produce a 2nd clutch of eggs, (B) the number of days between the end of family life and the production of the 2nd clutch eggs, (C) number of 2nd clutch eggs and (D) hatching rate of 2nd clutch eggs. Box plots depict median (middle bar) and interquartile range (light bar), with whiskers extending to 1.5 times the interquartile range and dots representing experimental values. Different letters refer to $P < 0.05$, ns refers to $P > 0.05$.