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Cadmium triggers hormesis in rice moth *Corcyra cephalonica* but different effects on two *Trichogramma* egg parasitoids

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With 4 figures and 1 table

Abstract: Increasing awareness of cadmium (Cd) pollution in agroecosystems has highlighted the need for a better understanding of the cascading effects heavy metals on the fitness of herbivores and their natural enemies, as well as the potential impact on the efficacy of integrated pest management (IPM). In this study, we assessed the bottom-up effects mediated by Cd on two important egg parasitoids, *Trichogramma japonicum* and *T. dendrolimi* via their factitious host, the rice moth *Corcyra cephalonica*. Results showed that the bottom-up effects mediated by Cd are complex. Cd exposure at 20 mg/kg in artificial diets of rice moth larvae enhanced the weight of eggs laid once they have reached adulthood, increased the proportion of females produced, and stimulated reproduction, thus suggesting a hormesis response. A stimulation effect on *T. dendrolimi* fitness was also found (when developing from contaminated rice moth eggs), but *T. japonicum* instead had a reduced fitness. In addition, unexposed adult parasitoids (reared from uncontaminated hosts) were not able to discriminate between uncontaminated or contaminated eggs (produced by rice moths reared on Cd-diet). Our results show that Cd contamination should not interfere with the effectiveness of inundative releases of *T. japonicum*, but the capacity of the subsequent F_1 generation of parasitoids in controlling pest populations could be affected by Cd contamination. This suggests that inundative releases should be favored over inoculative releases in Cd-contaminated sites, and mixed-species releases of *Trichogramma* could increase the cost effectiveness of pest biological control.

Keywords: heavy metals; stimulation; bottom up; biological control; sublethal effect

1 Introduction

Biological control agents have been successfully mass-reared and inundatively released in a variety of crops under variable environmental conditions, acting as efficient biopesticides in integrated pest management (IPM) programs (Huang et al. 2020; Zang et al. 2021). However, the efficacy of population suppression of agricultural pests by biocontrol agents is indirectly yet profoundly affected by abiotic environmental factors, including irrigation, fertilization, and soil pollutants (Han et al. 2015, 2022; Yan et al. 2023). Over the past two decades, such bottom-up effects have been shown to contribute to, or inhibit, sustainable pest control (Butler et al. 2009; Han et al. 2022).

Heavy metals are important pollutants in soil, triggering multiple bottom-up effects in agroecosystems (Dar et al. 2019; Liu et al. 2023; Yan et al. 2023). Cadmium (Cd) is one of the most important metal contaminants due to its relative toxicity threatening human health, a propensity to bioaccumulate, and a widespread occurrence in many agricultural systems (Hussain et al. 2021; Yu et al. 2022). This metal is readily assimilated by many crop plants and frequently transfers to phytophagous insects through feeding (Lin et al. 2020; Chen et al. 2022). Most often, Cd exposure causes chronic toxicological effects on growth and reproduction of phytophagous insects in a dose-dependent fashion (Butler & Trumble 2008; Wei et al. 2020; Di et al. 2016; Chen et al. 2022; Godinho et al. 2023). In addition, Cd can be transferred

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to predators or parasitoids of phytophagous insects (Naikoo et al. 2021; Tan et al. 2023). Natural enemies exposed to heavy metals typically live shorter lives, have a slower development, and exhibit a reduced reproductive potential (Gardiner & Harwood 2017). Studies have mainly focused on the effect of Cd accumulation on predatory insects (Dar et al. 2019; Naikoo et al. 2021). Because most parasitoids are typically more specialist than predators, they could be more vulnerable to Cd due to their inability to switch to alternative hosts (Tan et al. 2023). However, evidence on the effects of Cd exposure on parasitoids and Cd accumulation through the food chain is still lacking and there is a need for additional research to document how parasitoids respond to Cd contamination in their hosts.

Insects usually face many stressors at low levels in agroecosystems, and exposure to mild stress is now well known to induce hormetic effects in insects, i.e., a positive effect enhancing individual fitness (Cutler et al. 2022). Hormesis indicates a biphasic dose response with biologically positive effects at low doses and negative effects at high doses beyond the toxicological threshold (Agathokleous et al. 2023b). Hormetic effects induced by insecticide use have been widely reported in plants, herbivorous insects, and bees (Guedes et al. 2016; Cutler et al. 2022). Increased reproduction, enhanced longevity, and increased growth are the most frequently reported hormetic effects in pest insects following exposure to mild stress, and this can increase the occurrence of insecticide resistance and pest outbreaks (Guedes et al. 2016). Such hormetic effects also have been measured in biocontrol agents (Desneux et al. 2007). For example, exposure to low doses of pesticide stress has been shown to stimulate longevity, reproduction, and/or biocontrol service of predators and parasitoids (Ray et al. 2022; Wang et al. 2022). However, the indirect effect of heavy metal-mediated hormesis has been comparatively much studied; especially the potential hormetic effects induced by Cd in biocontrol agents via their specialist host remains largely unknown.

Egg parasitoids in the genus *Trichogramma* are among the most used biocontrol agents in IPM programs worldwide (Wang et al. 2014; Zang et al. 2021). *Trichogramma japonicum* Ashmead and *Trichogramma dendrolimi* Matsumura have been mass-reared and widely used for biological control of lepidopteran pests in rice fields in China (Wang et al. 2021a, 2022). While *T. dendrolimi* has a larger host range than *T. japonicum* (Lin 1994), *T. japonicum* is the most effective parasitoid of rice pests in China. As the cost of rearing *T. dendrolimi* is only 1/75 of that of rearing *T. japonicum*, they are used in optimal mixed releases against rice pests, which is much cheaper than *T. japonicum* released alone (Zang et al. 2021). Natural populations of *Trichogramma* play a major role in controlling economically important lepidopterous pests in agricultural crops in China (Wang et al. 2014; Zang et al. 2021). However, these parasitoids may be sensitive to environmental pollution. An increasing number of studies have reported sublethal stimulation and hormetic responses of arthropod parasitoids and parasitoids following exposure to pesticides and other contaminants (Wang et al. 2022; Agathokleous et al. 2023b). In China, rapid industrialization during the last three decades has resulted in widespread contamination of Cd in agricultural soils with 2.79 million hectares contaminated through atmospheric deposition, irrigation and livestock manure (Zhao et al. 2015; Liu et al. 2016; Hussain et al. 2021; Ren et al. 2022). Studies have confirmed that heavy metal contamination has a deleterious impact on the species richness and/or abundance of wild bees (Moroń et al. 2012; Shi et al. 2023). Essentially nothing has been reported regarding the potential bottom-up effects of Cd on *Trichogramma*.

In this context, we assessed the bottom-up effects of Cd to *Trichogramma* via their factitious host – mass-reared host to rear parasitoid biocontrol agents, the rice moth *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). We first examined the effect of Cd on the growth and development of the rice moth. Subsequently, the effects host Cd-contamination on the performance of *T. japonicum* and *T. dendrolimi* on *C. cephalonica* were evaluated by assessing parasitism rate, percentage of adult emergence, and production of female progeny. Moreover, the transfer and accumulation of Cd in the rice moth were also documented.

2 Material and methods

2.1 Insects

The rice moths *C. cephalonica* were reared in a temperature-controlled insectary (26 ± 1 °C, 60 ± 5% RH, 14:10 L:D photoperiod) in the Laboratory of Applied Entomology, Institute of Plant Protection, Beijing Academy of Agricultural and Forestry Sciences, China. They were reared on artificial diet (Di et al. 2018), and the rearing process was conducted following the procedures of Du et al. (2018). The parasitoid species *T. japonicum* and *T. dendrolimi* were maintained and reared using UV-irradiated *C. cephalonica* eggs (factitious hosts) under laboratory conditions (26 ± 1 °C, 70 ± 5% RH, 16:8h L:D) as Wang et al. (2021a) described. Newly emerged *Trichogramma* adult females were mated within 8 h and used for the experiments.

2.2 Rice moth performance on artificial diet exposed to cadmium

Based on previous research describing effects of cadmium on *Pyralidae* and *Galleriinae* (Ortel 1995; Zhang et al. 2017; Liu 2020), we used Cd^{2+} concentrations in artificial diets of 0 (control) and 20 mg of Cd^{2+}/kg_{DM}. For comparison, species known to accumulate cadmium can exceed 400 mg/kg_{DM} (Haag-Kerwer et al. 1999; Dos Santos Utmazian & Wenzel 2007) and rice shoots grown in polluted soil can exceed 30 mg/kg_{DM} (Murakami et al. 2009). Previous research has also shown that Cd exerts bottom-up effects on herbivores according to the amount accumulated, independently of the form of Cd added (Godinho et al. 2023). For our study, 50 mg cadmium chloride ($CdCl_2$, Shanghai Aladdin Bio-Chem Technology Co., LTD, China) was dissolved in 5 mL distilled water, and incorporated homogeneously into 2.5 kg artificial diet to make the Cd-containing artificial diets. The same volume of distilled water was added to the control diet. Following Di et al. (2018), the artificial diet was placed evenly (to approximately 30 mm) in a white plastic feeding box (45 cm × 35 cm × 5 cm, length × width × height), and rice moth eggs (0.5 mL, about 10,000 eggs) collected on the same day were evenly sprinkled on the diet. Then the feeding box was labeled, sealed with gauze, and placed in an air-conditioned insectary (26 ± 1 °C, 60 ± 5% RH, 14:10 L:D photoperiod). Each treatment (control, Cd treatment) was replicated ten times. The development duration of rice moths from egg to adult was recorded. After the adults emerged, the numbers of males and females were recorded, and the eggs laid in each box (replicate) were collected and counted daily.

2.3 Biological traits of rice moth eggs exposed to cadmium

Fifty newly emerged female adults of each treatment were weighed individually (XPR404S, Mettler Toledo, China), and then introduced into ventilated plastic cylindrical tubes (3.0 cm in diameter and 10 cm in length) individually to measure reproduction. The eggs laid within the first 24 h in each replicate were measured to determine the length, width, and weight of the eggs. The length and width of eggs were photographed and measured individually with a digital microscope (VHX-6000, Keens, Japan), and the size of eggs was measured based on the transection area: $S = \pi * a * b$, in which a and b are the length and width of eggs, respectively. The weight of 50 eggs per replicate was measured by using a balance (XPR2/AC, Shenbei Scientific Instrument Co., Ltd, China). Thirty eggs per replicate were placed into ventilated plastic cylindrical tubes (3.0 cm in diameter and 10 cm in length), examined, and removed daily. The total number of hatched eggs was used to determine the hatching rate.

2.4 Parasitism and performance of *Trichogramma* on Cd-exposed hosts

A no-choice experiment was conducted to determine the parasitism by *T. japonicum* and *T. dendrolimi* on Cd-exposed and unexposed *C. cephalonica* eggs. We introduced five newly emerged *T. japonicum* females into a ventilated plastic cylindrical tube (3 cm in diameter and 10 cm in length) which contained a card loaded with 250 cadmium-exposed or 250 unexposed eggs. Cd-exposed eggs correspond to eggs laid by rice moth females reared on a Cd-contaminated diet. Each tube contained a small piece of cotton wool with 15% honey solution and was maintained under insectary conditions at 26.0 ± 1.0 °C and 60 ± 5.0% RH. After 6 h (from 12:00 to 18:00 at 3000 Lux), each *Trichogramma* female was removed. If the female died, the replication was discarded. The experiment was conducted under laboratory conditions (26 ± 1 °C, 60 ± 5% RH, 16:8h L:D photoperiod) with 15 replicates for Cd-exposed and Cd-unexposed eggs each. The egg cards were monitored daily for five days, and newly hatched rice moth larvae were gently removed from the card using a brush to avoid disturbing egg parasitism by female parasitoids. Then, egg cards were examined under a stereoscopic microscope, and the numbers of parasitized eggs (black) were recorded (Du et al. 2018). The egg cards were continuously examined every day until all parasitoids had emerged and died, and the percentage of adult emergence was calculated as the number of adult emerging divided by the number of host eggs parasitized. All emerged adults were sexed to also calculate the sex ratio for each egg card. In each treatment, 60 emerged *Trichogramma* female adults were randomly selected to measure the individual size (body length and hind tibia length) using a digital microscope (VHX-6000, Keens, Japan). Body length and hind tibia length are important parameters to characterize the parasitic fitness of *Trichogramma* parasitoids (Wang et al. 2020).

2.5 Parasitism and performance of *Trichogramma* exposed to Cd-exposed hosts

A no-choice experiment was conducted to determine the performance of *T. japonicum* and *T. dendrolimi* on *C. cephalonica* eggs produced by females that developed on Cd-contaminated diet (Cd-exposed eggs). The *Trichogramma* adults used in the experiments were from two groups: either adults developing from eggs that were not exposed to Cd (simulating factitious hosts used for parasitoid mass-rearing) or adults developing from larvae grown on a Cd-contaminated artificial diet (simulating those developing from a rice moth field population at a contaminated site). The experiment was conducted as described in the previous test. The numbers of parasitized eggs (black), emerged females, and male adults per card were counted. The percentage of adult emergence and female progeny was calculated.

2.6 Cadmium accumulation of rice moth and *Trichogramma* wasps

Rice moth samples (2 larvae in the late sixth instar, 2 female adults, 15 male adults, and 1.5 mL eggs for one replication; 5 replicates for each development stage) were dried at 65 °C for 48 h, and ground into a fine powder. Samples (0.05 g of larvae, 0.02 g of female adults, and 0.08 g of eggs) were digested in 10 mL of 10:1 nitric acid: perchloric acid solution at 170 °C for 30 min. The digested samples were filtered and diluted to 25 mL with 5% nitric acid. The Cd content in each sample was analyzed by inductively coupled plasma source mass spectrometer (ICP-MS) (iCAP RQ, Thermo Scientific, USA) in the standard (STD) mode.

Due to the small size of *Trichogramma* parasitoids, a super microwave digestion system (EXPEC 790S, Hangzhou EXPEC Technology Co., Ltd, China) was used to make the sample digestion process more efficient. A total of 800 females of *Trichogramma* parasitoids was used in each replicate, and three replicates for each species were prepared. Samples were dried at 65 °C for 48 h, and digested in 2 mL of nitric acid at 240 °C for 20 min with 4 MPa programmed pre-pressurization to effectively suppress sample bumping during heating process. The digests were brought to a final volume of 5 mL by adding 5% nitric acid. The Cd content in each sample was analyzed by ICP-MS (SUPEC 7000, Hangzhou EXPEC Technology Co., Ltd, China). Commercially available standard Cd solutions preserved in nitric acid were used to prepare the calibration standards.

2.7 Data analysis

All data were subject to normality testing (Shapiro-Wilk test, $P < 0.05$) and homoscedasticity (Levene's test, $P < 0.05$) before analysis of variance. Percentage data for adult emergence or female progeny were transformed to arcsine square root prior to the normality test. A Student's t test was used to analyze the data between control and Cd treatment at $P < 0.05$. Statistical analyses were performed using the SPSS statistical software package (var. 25.0, IBM, USA).

3 Results

3.1 Rice moth performance on Cd-contaminated artificial diet

Cd exposure through artificial diet significantly increased (+10%) the total number of rice moth adults emerging (from 2310 eggs in control in average to 2559 eggs when Cd-exposed), but the effect on adult longevity and female fecundity was not significant (Fig. 1A–C). Furthermore, Cd exposure resulted in a significant increase by 13% in adult female weight (from 37 mg to 42 mg in average) and the proportion of females (from 44% to 54% in average) in the resulting population (Fig. 1D, E). Interestingly, the total number of eggs laid by females from the Cd-exposed group was significantly higher by 1.4 times than that from the untreated control group (from 176,800 to 251,000 in average; Fig. 1F).

3.2 Biological traits of rice moth eggs from adults reared on Cd-containing diet

Adult rice moths reared on Cd-contaminated diet produced significantly larger (from 0.16 to 0.17 mm in aver-

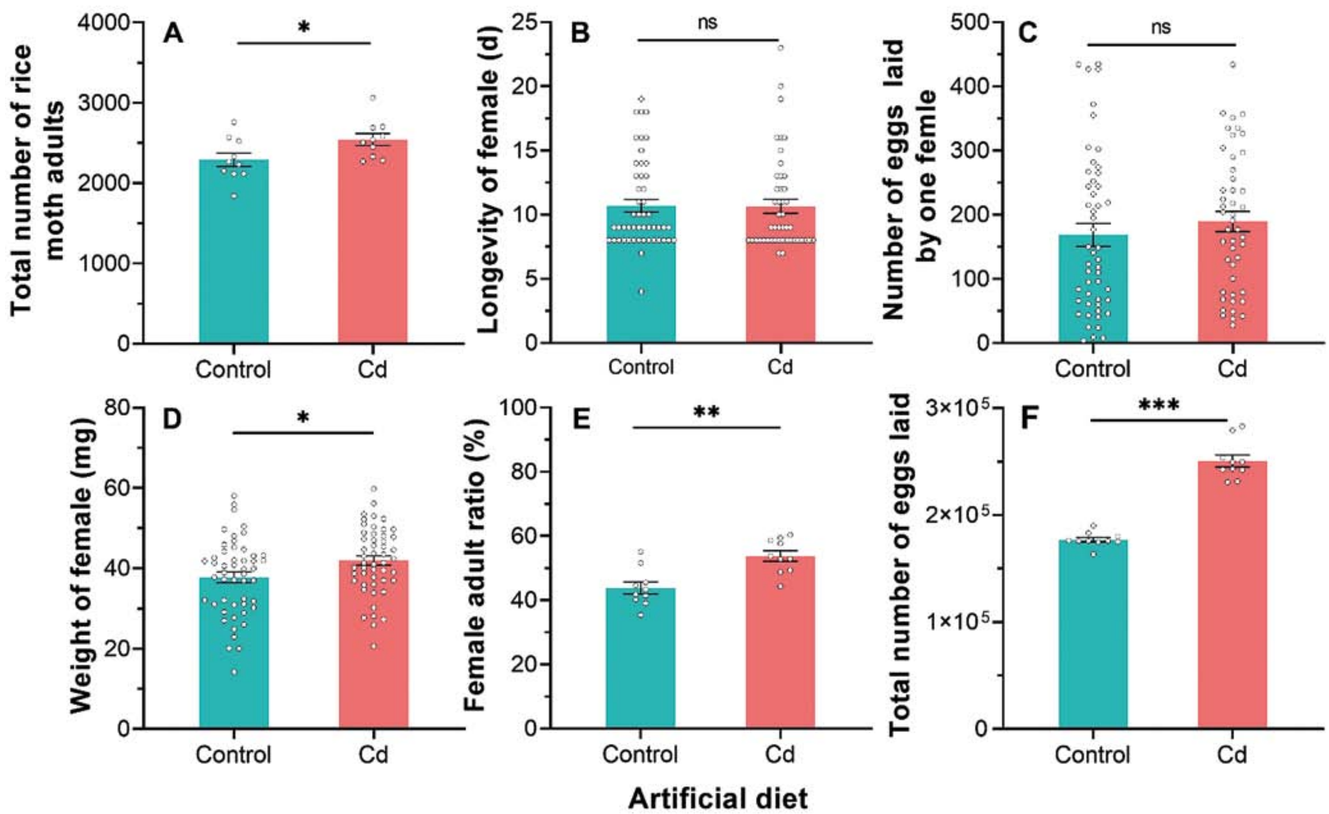

Fig. 1. Effects of Cd exposure on the growth of rice moths. The total number of rice moth adults emerged (**A**), longevity of female adults (**B**), number of eggs laid by one female (**C**), adult female/male ratio (**D**), weight of adult females (**E**), and total number of eggs produced (yF) in treatment with Cd-contaminated artificial diet (Cd) or not (control) (mean ± SD). (ns, not significant; **P* < 0.05; ***P* < 0.01; ****P* < 0.001, Student's *t* test).

age) and heavier (from 1.83 mg to 2.09 mg in average) eggs (Fig. 2A, B) as compared to those reared on uncontaminated diet. However, the numbers of eggs successfully hatching into first stage larvae did not differ between Cd-exposed rice moths and control (Fig. 2C).

3.3 Effect of Cd exposure on performance of *T. japonicum* parasitizing *C. cephalonica*

There was no significant difference in the number of rice moth eggs parasitized by *T. japonicum* between Cd-exposed and control eggs (Fig. 3A). However, significantly fewer eggs were parasitized when *T. japonicum* had been exposed to Cd during development (reared from Cd-exposed eggs) regardless of whether the eggs were exposed to Cd (22% reduction, from 127 to 99 eggs in average) or not (40% reduction, from 135 to 81 eggs in average; Fig. 3A). Cd exposure to *T. japonicum* induced a significantly higher percentage of female progeny (from 70 to 77% in average) but a 10% lower emergence rate (from 82% to 74% in average; Fig. 3B, C). Thus, effectiveness of *T. japonicum* parasitoids emerging from non-contaminated eggs (such as used in insectaries) would not be impacted by eggs found in either control or low-level Cd-contaminated sites, but parasitoids emerging from eggs at contaminated sites would have reduced effectiveness no matter if the host eggs they subsequently parasitized were exposed to Cd or not. Cd exposure in *T. japonicum* wasps during their development resulted in a significant decrease in body length by 6% (mean ± SD: unexposed wasps 513.3 ± 3.3; Cd-exposed wasps 481.8 ± 2.5) and hind tibia length by 5% (mean ± SD: unexposed wasps 152.9 ± 0.6; Cd-exposed wasps 143.9 ± 0.6), showing toxic effects and suggesting a reduced fitness in *T. japonicum*.

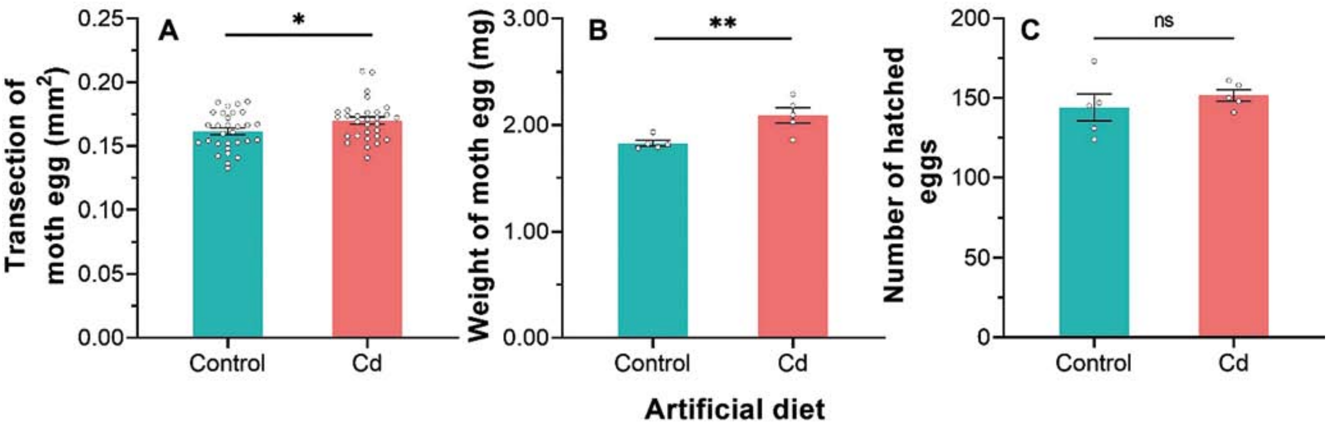

Fig. 2. The morphological characters and hatching of rice moth eggs from Cd-exposed larvae. The size (**A**), weight (**B**), and hatched number (**C**) of rice moth eggs from larvae exposed to a Cd-contaminated diet (Cd) or not (control) (mean ± SD). (ns, not significant; *$P < 0.05$; **$P < 0.01$, Student's t test).

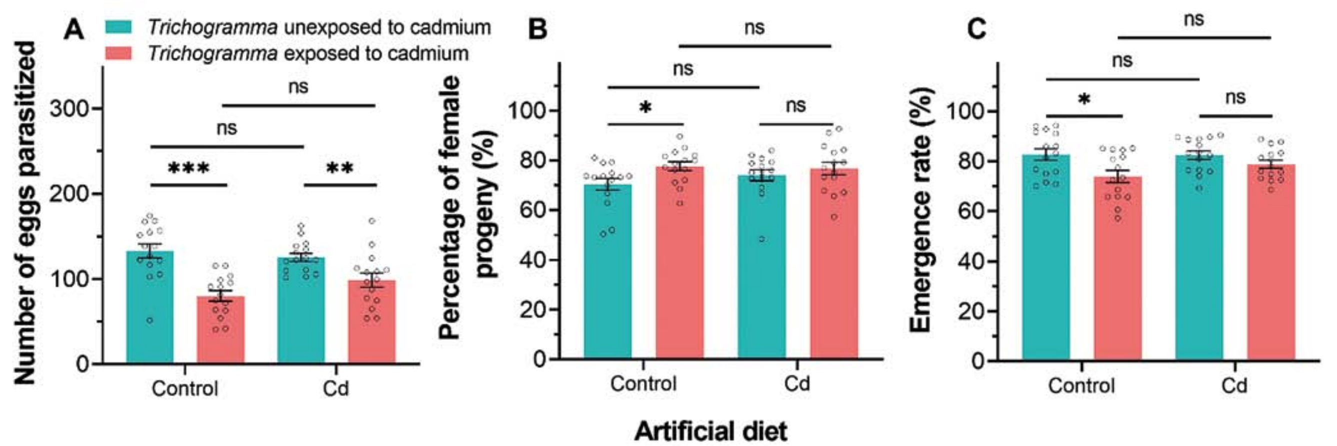

Fig. 3. Effect of Cd exposure on the parasitism and performance of *Trichogramma japonicum* on *C. cephalonica*. Number of rice moth eggs parasitized (**A**), percentage of female progeny produced (**B**), and emergence rate (**C**) of *T. japonicum* exposed to Cd during development (reared from Cd-exposed hosts; red) or not (blue), and when provided with Cd-contaminated eggs (Cd) or not (control) (mean ± SD). (ns, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$, Student's t test).

3.4 Effect of cadmium on performance of *T. dendrolimi*

Without Cd exposure during parasitoid development, *T. dendrolimi* did not show a significant difference in the number of eggs parasitized between Cd-exposed and unexposed eggs (Fig. 4A). However, when *T. dendrolimi* had been exposed to Cd during development, it parasitized significantly more eggs than the unexposed wasps no matter whether the eggs were exposed (+41%; from 137 to 220 eggs in average) or not (+37%; from 113 to 155 eggs in average), and it parasitized significantly more Cd-exposed than unexposed eggs (+33%; from 154 to 220 eggs; Fig. 4A). In addition, the proportion of female progeny in Cd-unexposed rice moth eggs issued from Cd-exposed wasps during their development was significantly lower by 8% than that issued from in Cd-unexposed wasps (77% in Cd-exposed, 84% in control wasps in average); however, there was no difference in sex ratio between Cd-exposed and unexposed wasps during their development when rice moth eggs provided were Cd-contaminated, but the percentage of female progeny from Cd-contaminated was 8% higher than that from Cd-unexposed eggs (84% versus 77% in average) when wasps that had been exposed to Cd during their development (Fig. 4B). No significant differences in emergence rate of *T. dendrolimi* were found (Fig. 4C). Finally, Cd exposure did not influence body length (mean ± SD: unexposed wasps 524.5 ± 4.4; Cd-exposed wasps 525.7 ± 4.2) nor hind tibia length (mean ± SD: unexposed wasps 152.1 ± 0.3; Cd-exposed wasps 151.3 ± 0.5) in *T. dendrolimi*. These results show that Cd exposure could induce a hormesis effect in *T. dendrolimi*, with no direct negative effects.

3.5 Analysis of the cadmium content and transfer effects

Cd exposure at 20 mg/kg in artificial diets resulted in Cd transfer from artificial diet to larvae, females, and eggs of rice moths (Table 1). In addition, *T. japonicum* females emerging from Cd-contaminated hosts were significantly enriched in Cd, but not *T. dendrolimi* females (Table 1). The transfer coefficients of Cd decreased with the developmental stages of rice moths (artificial diet to rice moth larva and female 0.35 and 0.09, respectively; diet to F1 rice moth egg 0.01; rice moth larva to female 0.25; rice moth female to F1 egg 0.13) and were always below 1, showing a bio-minimization effect.

4 Discussion

Soil pollution can trigger various indirect bottom-up effects and affect multitrophic interactions and the efficacy of IPM (Han et al. 2022). In this study, we found that the bottom-

Table 1. Cadmium concentrations (mean ± SD) in rice moth *Corcyra cephalonica* (CC) and *Trichogramma japonicum* (TJ) and *T. dendrolimi* (TD) females. DM: dry mass. n = 5 for CC, n = 3 per parasitoid species. ns: not significant, **: $P < 0.01$, ***: $P < 0.001$ (Student's test).

	CK (0 mg/kg)	Cd (20 mg/kg)
CC larva (mg/kg$_{DM}$)	0.016 ± 0.001	6.919 ± 0.519***
CC ♀ (mg/kg$_{DM}$)	0.039 ± 0.009	1.736 ± 0.127***
CC egg (mg/kg$_{DM}$)	0.088 ± 0.010	0.232 ± 0.030**
TJ (mg/800 ind.)	0.011 ± 0.002	0.026 ± 0.002**
TD (mg/800 ind.)	0.006 ± 0.001	0.005 ± 0.001ns

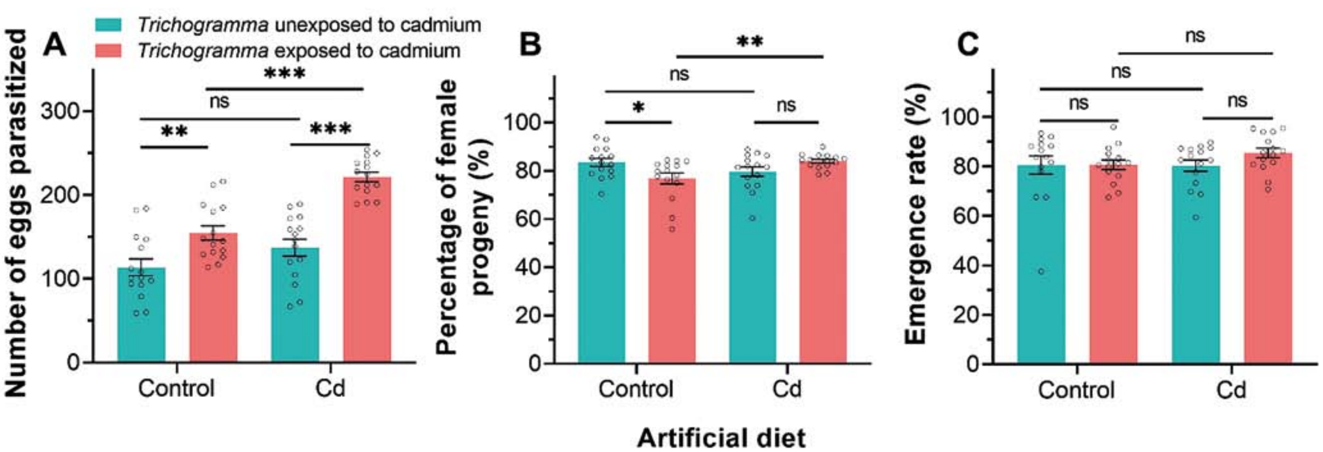

Fig. 4. Effect of Cd exposure on the parasitism and performance of *Trichogramma dendrolimi* on *C. cephalonica*. Number of eggs parasitized (**A**), percentage of female progeny (**B**), and emergence rate (**C**) of *T. dendrolimi* exposed to Cd during development (reared from Cd-exposed hosts; red) or not (blue), and when provided with Cd-contaminated eggs (Cd) or not (control) (mean ± SD). (ns, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$, Student's *t* test).

up effects mediated by low concentrations of Cd pollution on an herbivorous pest and its parasitoids are variable. Cd exposure at 20 mg/kg in artificial diets enhanced the weight, proportion of female offspring, and reproduction of females of the rice moth pest, suggesting a hormesis effect. In general, all of these enhanced characteristics could be expected to benefit rice moth populations. In addition, rice moth eggs produced by adults reared from larvae feeding on either Cd-contaminated or control diets were equally parasitized for parasitism by *T. japonicum* that had not been exposed to Cd (such as would be produced by insectaries). However, *T. japonicum* adults exposed to Cd during their development (i.e., reared from rice moth eggs produced by moths grown on Cd-contaminated diets) showed a reduced parasitism capacity regardless if provided with eggs were from a moth population exposed to Cd or not. Conversely, *T. dendrolimi* reared from Cd-exposed eggs parasitized a significantly higher number of eggs than the unexposed wasps.

Previous studies have documented that Cd exposure causes a variety of chronic toxic effects on the growth and reproduction of phytophagous insects, that are dependent on Cd concentrations (Wei et al. 2020; Chen et al. 2022; Godinho et al. 2023). For example, Su et al. (2014) reported that low doses of Cd promoted the increase of *Spodoptera exigua* (Lepidoptera: Noctuidae) populations, whereas high doses inhibited population growth. Increased reproduction is the most common hormetic effect in insects following exposure to mild stress (Cutler et al. 2022). Our results showed that Cd exposure to rice moth larvae in artificial diets not only enhanced the reproduction of the resulting adults, but also increased the size and weight of their eggs, suggesting potentially increased fitness of F_1 rice moths. Similar to our results, Nath et al. (2023) found that sublethal phosphine fumigation induced transgenerational hormesis in *C. cephalonica*. The disruption/modification of the courtship rhythm for females and copulation behavior found in some lepidopteran insects could partially explain the increased fecundity (Su et al. 2021). From a hormesis context, mild stress (e.g., sublethal doses of insecticides) has been shown to stimulate growth and/or reproduction of several pest species, which is a possible cause of pest resurgence and secondary pest outbreaks in IPM programs (Cutler et al. 2022; Agathokleous et al. 2023a). Heavy metal-induced hormesis in arthropods, despite a potentially widespread occurrence due to Cd contamination of large agricultural regions, has received far less attention than hormesis caused by insecticides (Cutler et al. 2022).

Studies have reported sublethal stimulation and hormetic responses of arthropod parasitoids in the presence of environmental contaminants (Wang et al. 2022; Agathokleous et al. 2023b). Heavy metal transfer along the food chain can affect the growth and behavior of predators and parasitoids (Naikoo et al. 2021; Chen et al. 2022; Tan et al. 2023). Although most studies have focused on predators, there are a few reports of the bottom-up effects mediated by Cd on the growth, development, and reproduction of parasitoids. Unlike phytophagous insects (and some predators), Cd cascades in food chains have mostly demonstrated non-toxic effects on parasitoids including *Ceratitis capitata* (Hymenoptera: Diapriidae) (Kazimírová & Ortel 2000), *Aphidius colemani* (Hymenoptera: Braconidae) (Konopka et al. 2013), and *Anagrus nilaparvatae* (Hymenoptera: Mymaridae) (Chen et al. 2022). A recent study reported that the number of larvae and the number of resulting adults of the pupal parasitoid *Chouioia cunea* (Hymenoptera: Eulophidae) decreased significantly after parasitizing Cd-contaminated *Hyphantria cunea* pupae (Tan et al. 2023). In our study, we measured Cd concentration in *Trichogramma* parasitoids and found that Cd concentrations were significantly enriched in *T. japonicum* females but not in *T. dendrolimi* females. These results are in accordance with the parasitism and performance of *Trichogramma* parasitoids exposed to Cd-contaminated hosts. Indeed, *T. japonicum* emerging from Cd-contaminated hosts have a reduced parasitism capacity, which may be due to the toxic effects of Cd exposure. However, there is no significant contamination of Cd in *T. dendrolimi*, and a positive effect on *T. dendrolimi* fitness was found with no negative effects, suggesting a hormesis response.

Although we measured reduced fitness parameters for *T. japonicum* adults exposed to Cd during their development, we also found that if *T. japonicum* adults were not exposed to Cd as immatures, *T. japonicum* fitness (number of eggs parasitized, percentage of female progeny, and emergence rate) was not affected regardless if the provided rice moth host eggs were Cd-contaminated or not. The lack of response to either contaminated or uncontaminated prey eggs suggests that *T. japonicum* adults do not recognize Cd presence in the eggs they parasitize. As for *T. dendrolimi* reared from Cd-contaminated eggs, they were able to parasitize more eggs than those reared from Cd-uncontaminated eggs, which would induce higher host mortality and increased pest control. In addition, there was no significant difference in the emergence rate of *T. dendrolimi* from Cd-contaminated or uncontaminated hosts. This shows that *T. dendrolimi* pre-exposed to Cd could be a more efficient biocontrol agent against rice pests in Cd-contaminated fields. The variable results across parasitoid species observed in the literature and in our study indicate that it is critical to measure the fitness of adult parasitoids reared from contaminated food sources, and not just measure the fitness of uncontaminated adults provided with contaminated versus uncontaminated prey. We also recognize that more evidence at a larger scale (such as caged and open field studies) are needed to verify the results seen in the laboratory.

The physiological mechanism(s) that reduces parasitism by *T. japonicum* reared on Cd-contaminated hosts is not clearly understood. Such decreased parasitism may result from a direct toxicity of Cd or an indirect effect induced by Cd (e.g., increased host immunity). Although the latter may be lowered in factitious hosts, it could play in the field, but our results are valid for mass rearing conditions. Parasitoid wasps lay eggs in or on the bodies of their hosts and regulate the energy metabolism of their hosts to match their own specific nutrition requirements (Wang et al. 2021b). Due to the strong dependence on hosts to complete their development, parasitoid wasps are susceptible to the presence of toxic chemicals in their hosts. Cd-induced immune toxic effects and energy metabolism disorders have been reported in lepidopterans and pupal parasitoids (Wei et al. 2020; Tan et al. 2023), but this has not been reported for *T. japonicum* or in any egg parasitoid. Moreover, the two *Trichogramma* species showed different responses under Cd exposure, both in terms of Cd accumulation and fitness consequences, where *T. japonicum* accumulated Cd from Cd-contaminated larvae and with negative fitness consequences while this was not the case in *T. dendrolimi*. This may result from their different biology. These wasps have a similar morphology, size, and generation time but differ greatly in host range: *T. dendrolimi* has a larger host range than *T. japonicum* (Lin 1994). Host range shift is one of the main eco-evolutionary forces driving speciation, and during this process species divergence may lead to differences in physiological responses to environmental stressors (Forbes et al. 2017; Chen et al. 2021). The solitary generalist parasitoid *Leptopilina heterotoma* has a higher capacity to manipulate the immunity behavior of its hosts than the specialist parasitoid *L. boulardi*. Such active immune suppression, which is absent in the specialist parasitoid, allows the generalist parasitoid to parasitize a broader host range (Huang et al. 2021). Our results suggest that that *T. dendrolimi* has a stronger tolerance to Cd exposure than *T. japonicum*, potentially resulting from the evolutionary adaptation to a wider host range. In addition, hormesis-like responses in *T. dendrolimi* could be used to optimize the mass rearing of biocontrol agents for field releases (Agathokleous et al. 2023b; Nath et al. 2023). Furthermore, the expression of cellular immunity genes, immune recognition genes, signal transduction genes, and antimicrobial peptide genes of hosts have been found to be related to a decreased fitness of parasitoids developing in Cd-contaminated hosts (Tan et al. 2023). Accurately determining the expression levels of related genes in rice moths and parasitoids would be a useful next step in documenting specific regulatory mechanisms triggered by Cd exposure and influencing pests' natural enemies.

Trichogramma species are among the most naturally-abundant egg parasitoids in China, where they play a key role in controlling economically-important lepidopterous crop pests (Wang et al. 2014; Zang et al. 2021). *Trichogramma* species diversity has been experiencing a rapid decline in China's corn agroecosystems over a 30-year time period (Hu et al. 2023). Cadmium bottom-up effects may have contributed to this biodiversity decline, similar to wild bees (Moroń et al. 2012; Shi et al. 2023). For instance, Shi et al. (2023) found that there were significant negative correlations between heavy metal pollution and wild bee diversity and species richness. Our study found that Cd exposure by hosts induced opposite effects on the two *Trichogramma* species, resulting in reduced parasitism of *T. japonicum* but enhanced parasitism of *T. dendrolimi*. These results indicated that heavy metal pollution may lead to the decline in the diversity of egg parasitoids, and specifically *Trichogramma* in Cd-contaminated agroecosystems. This may in turn result in decreased biocontrol services, causing economic losses. Interestingly, we found that Cd exposure tended to increase the fitness of *T. dendrolimi* but it had negative effects on *T. japonicum*. This suggests that: (i) releases of *T. dendrolimi* rather that *T. japonicum* should be favoured at Cd-contaminated sites where *T. dendrolimi* could be a better-fit biocontrol agent; and (ii) inundative, rather than inoculative releases of *T. japonicum* should be used at Cd-contaminated sites. More efforts are required to assess the potential impacts of heavy metals on natural enemies (i.e., *Trichogramma*) in agroecosystems to ensure the maintenance of pest biological control services for crops. Notably, it is important to understand the dose-dependent response of biocontrol agents to heavy metal pollution, as well as the potential transgenerational effects.

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