

Insecticide-induced hormesis in a factitious host, *Corcyra cephalonica*, stimulates the development of its gregarious ecto-parasitoid, *Habrobracon hebetor*

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HIGHLIGHTS

- Sublethal concentrations of deltamethrin induce hormesis in the factitious host *Corcyra cephalonica*.
- Enhanced performance of the parasitoid *Habrobracon hebetor* was observed on the hormetic host *C. cephalonica*.
- These observations might be helpful in mass rearing of *H. hebetor* as a biocontrol agent.

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ABSTRACT

Hormesis phenomena in insect pests can have a negative impact, but for beneficial insects, it might be used to optimize mass rearing and increase the quality of biocontrol agents. Here, we report the multigenerational stimulatory effects of deltamethrin in a factitious laboratory host, *Corcyra cephalonica*, and the subsequent performance of its parasitoid, *Habrobracon hebetor*. The effects of sublethal (LC₁₀), low lethal (LC₁₅, LC₂₀, LC₂₅ and LC₃₀) and median lethal (LC₅₀) concentrations of deltamethrin along with the control were evaluated on biological traits and nutrient reserves of the host for three consecutive generations (G₀, G₁, and G₂). The biological traits of *C. cephalonica* (fecundity, developmental duration and larval weight gain) did not differ significantly in the parental generation (G₀), whereas in the later generation (G₂), significant differences were observed with the control. Nutrient reserves (protein and lipid content) in *C. cephalonica* were significantly influenced by sublethal concentrations in all three generations (G₀, G₁, and G₂). The performance of *H. hebetor* on the factitious host *C. cephalonica* (G₂) revealed a significant increase in parasitoid fecundity of 65% when host larvae were exposed to LC₁₅. However, no difference in hatch and pupation rates of parasitoids were observed across treatments. The emergence of both males and females and the longevity of only female wasps were significantly different. No effects were observed on male longevity. Taken together, insecticide-induced hormesis in host *C. cephalonica*, especially at LC₁₅ exposure, stimulates the development of parasitoid *H. hebetor* without obvious major trade-off. The results might be helpful in mass rearing of *H. hebetor* as a biocontrol agent.

1. Introduction

Agricultural insects are generally exposed to insecticides through

direct application or ingestion through food or residual contact (Stark and Banks, 2003; Desneux et al., 2005, 2007). Apart from lethal effects, chemical insecticides can have sublethal effects in exposed arthropods

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(Desneux et al., 2007; Fogel et al., 2013; Yao et al., 2015; Ullah et al., 2019a). These effects may impact various demographic traits and ultimately the growth of these arthropods (Desneux et al., 2006; Jam and Saber, 2018; Zhang et al., 2019; Gul et al., 2019; Ullah et al., 2019b, 2019c; Chi et al., 2020). The effects of insecticides on target and nontarget insect populations depend on several factors; nonetheless, the dose is a key factor of response (Cutler, 2013; Decourtye et al., 2013). Pesticides are generally applied at sufficient concentrations to kill target insect pests, but spatiotemporal changes in concentrations due to abiotic and biotic factors lead to altered targeted doses (Desneux et al., 2005). These altered doses/concentrations (sublethal) often stimulate metabolic processes and, ultimately, the growth of organisms (Calabrese, 2010). This biological phenomenon is termed 'hormesis'. Hence, sublethal and low lethal effects should be considered when estimating the total effect of any insecticide, including biorational and botanical pesticides (Desneux et al., 2007; Guedes et al., 2016; Haddi et al., 2020). These effects could be lethal and acute or sublethal and chronic, resulting in changes in insect physiology and ultimately development (Sak et al., 2009).

The rice moth *Corcyra cephalonica* (Lepidoptera: Pyralidae) is an important insect pest of stored rice and other products in tropical regions (Harita et al., 2000). The larvae cause damage to grains by forming silken webs and feeding inside them. Deltamethrin has been widely used as a primary chemical to manage this pest. The Food Corporation of India has recommended treating produce with deltamethrin once every three months as a prophylactic measure (FCI, 2020). *Corcyra cephalonica* is also one of the most preferred hosts for the mass production of egg and larval parasitoids of the hymenopteran families, viz. Trichogrammatidae, Braconidae, Bethyridae, and Platygastridae (Jalali and Singh, 1992; Singhamuni et al., 2016; Pomari-Fernandes et al., 2015; Nasrin et al., 2016; Queiroz et al., 2017). Commercial mass rearing of beneficial insects is a multibillion-dollar industry. Unfortunately, in recent days, biological pest management has experienced a shortage of quality natural enemies, leading to declines in the rates of success (Lenteren and Tommasini, 2003; Alvarez et al., 2019; Barratt et al., 2018). Hormesis phenomena may be exploited during the mass rearing of insects to enhance biological traits (longevity, fecundity, etc.). Several studies have proven that exposure to low doses of insecticide can boost reproduction or oviposition of insect natural enemies, including the parasitoid *Habrobracon hebetor* (Grosch and Vacovic, 1967; Guedes et al., 2009; Xiao et al., 2016; Cutler and Guedes, 2017). Similarly, exploitation of hormetic responses could be useful during mass rearing to resist pathogens (Etzel and Legner, 1999).

Habrobracon hebetor (Say, 1836) (Hymenoptera: Braconidae) is a cosmopolitan, gregarious, idiobiont, larval ectoparasitoid of mainly obtectomeran families of Lepidoptera (Borzoui et al., 2016; Singh et al., 2009). The parasitoid attacks some of the important insect pests of field crops and stored products, including *C. cephalonica* (Farahani et al., 2016a, 2016b; Yu et al., 2003). Many insectaries use *C. cephalonica* as a host of choice for mass rearing of *H. hebetor*. The parasitoid *H. hebetor* has a short generation time, a high reproductive rate, and many host species.

Insecticides affecting host plant-arthropod pest interactions and plant-pest-natural enemy interactions are potentially important (Guedes et al., 2016). Food intake may represent the major route for toxic incorporation in animals. These food web-mediated effects indirectly affect the response and performance of animals to toxic exposure (Wang and Wang, 2006; Hjorth et al., 2007). Few previous studies have reported host-mediated effects of toxic chemicals in different organisms. Saiz et al. (2009) reported the sublethal effects of naphthalene and 1, 2-dimethylnaphthalene on the marine cyclopoid copepod *Oithona davisae* (Copepoda: Cyclopoida) through its food. Concerning braconid parasitoids, similar studies were reported in *Cotesia marginiventris* (Hymenoptera: Braconidae). The Cry1Ab protein introduced to the host, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), and the Cry1Ac protein introduced to *Pseudoplusia includens* (Lepidoptera: Noctuidae) had

negative effects on *C. marginiventris* (Baur and Boethel, 2003; Ramirez-Romero et al., 2007).

Of late, sublethal effects on natural enemies have received the most attention because of their integrated pest management value. Despite advances in the chemical management of *C. cephalonica*, there is still inadequate information on the sublethal and low lethal effects of deltamethrin on the targeted pest and its parasitoid *H. hebetor*. Several studies have reported insecticide-induced sublethal and low lethal effects on *H. hebetor* (Abedi et al., 2014; Ali et al., 2014; Asadi et al., 2018a, 2018b; Rashidi et al., 2018). These studies have reported stimulatory effects or hormesis directly in parasitoids, but for the first time, our study attempts to understand host (*C. cephalonica*)-mediated sublethal and low lethal effects in parasitoid (*H. hebetor*). Moreover, experiments indicating stimulatory responses in beneficial natural enemies seem limited to a single generation. Therefore, in the current study, the effects of sublethal and low lethal concentrations of deltamethrin over generations on key biological traits of the factitious host *C. cephalonica* and the developmental performance of the parasitoid *H. hebetor* via its host were investigated. The results of this study might be useful in enhancing the mass rearing of *H. hebetor* by biocontrol producers.

2. Material and methods

2.1. Study environment

The study was carried out in the Biocontrol Laboratory, Division of Crop Protection, ICAR-National Rice Research Institute (NRRI), Cuttack, India (20°27'14.0"N 85°56'06.0"E) under controlled conditions (temperature 25 ± 1 °C; relative humidity 70 ± 5%; and 14 h light:10 h dark). Parameters were measured with an indoor thermometer/hygrometer (HTC-1).

2.2. Source and rearing of factitious host

The initial colony of the factitious host, *C. cephalonica* unexposed to pesticides, was obtained as eggs from the ICAR-National Bureau of Agricultural Insect Resources, Bengaluru, India (National Accession Number: NBAII-MP-PYR-01). Host insects were reared as per the modified method of Lalitha and Ballal (2015) with maize as their diet (Chaudhuri and Senapati, 2017). To mass rear *C. cephalonica*, 0.25 cc (~5000 eggs) of eggs were charged on a medium consisting of sterilized and insecticide-free broken kernels of maize (2.5 kg), roasted groundnut seeds (50 g), multivitamin powder (5 g), yeast (2 g), streptomycin sulphate (0.2 g) and formalin (0.1%; 10 mL). After adult emergence, moths were collected through a vacuum suction system (motor power: 120 W) consisting of an outer plastic circular container (50 L) and an inner oviposition chamber (10 L) covered with wire mesh on its base to drop the eggs. A cotton swab dipped in 50% honey was stuck on the inner wall of the oviposition chamber. The eggs collected were maintained on a fresh diet for rearing. More than 10 generations were reared before larvae were used in subsequent experiments.

2.3. Source and rearing of parasitoids

An initial mother colony of parasitoids, *Habrobracon hebetor* unexposed to pesticides, was collected as pupae (~300) from the National Institute of Plant Health Management (NIPHM), Rajendranagar, Hyderabad, Telangana State, India. To mass rear parasitoids, immediately after adult emergence, a pair of parasitoids was placed in a plastic container (1000 mL) for mating. After 24 h of mating, five late instar larvae (4th and 5th instar) (Hagstrum and Smittle, 1977) of *C. cephalonica* were introduced between two layers of fine muslin cloth and placed over the mouth of the container (referred to as the 'sandwich method') (Ghimire and Phillips, 2014). Adult parasitoids could feed on honey that was provided through sterilized cotton swabs. Female parasitoids were allowed to attack the host larvae for 48 h, and parasitized larvae were

incubated for further development under standard laboratory conditions (temperature 25 ± 1 °C; relative humidity $70 \pm 5\%$; and 14 h light:10 h dark). After the fifth generation of continuous rearing, adult parasitoids (0–12 h old) were utilized for experiments to avoid the carry-over effect, if any.

2.4. Insecticide

A commercial formulation of the insecticide deltamethrin 2.5% WP (Delthrin®; Hernba industries limited) was used in the experiments. The bioassays were conducted with fresh solutions of deltamethrin prepared in deionized water. Insecticide was selected based on its use for the control of *C. cephalonica* as recommended by the Central Insecticide Board and Registration Committee, Government of India (CIBRC, 2020). Deionized water was used as a negative control in all experiments. All insecticide dilutions used in the bioassay were fresh to avoid chemical decomposition.

2.5. Determination of the dose–response curve

To estimate the LC_{50} of deltamethrin for *C. cephalonica* larvae, a preliminary concentration-setting bioassay was carried out to determine the appropriate ranges of concentrations. At 25 mg L^{-1} , no larval mortality was observed, whereas at 50 mg L^{-1} , 11.07% mortality and at 500 mg L^{-1} , more than 95% mortality was observed. Hence, six increasing concentrations were selected, i.e., 50, 100, 200, 300, 400, and 500 mg L^{-1} , for the bioassay ($N = 210$). The 20 g diet of *C. cephalonica* (as mentioned in 2.2) was placed in Petri dishes and mixed thoroughly with the respective concentrations of insecticide at a rate of 0.1 mL g^{-1} of diet and allowed to air dry (Oluwafemi et al., 2009). There were seven treatments, ten 4th instar *C. cephalonica* larvae (Khani et al., 2012) were introduced in each replication, and three such replications were maintained per treatment. Petri dishes were sealed with Parafilm (Fisher Scientific, Ottawa, Canada) to prevent insect escape. All replicates were placed in an insect growth chamber (model: JSPC-420C; JS Research Inc. Republic of Korea) set at 25 °C, 70% RH, 14L:10D. Larval mortality was assessed after 48 h of treatment. Concentrations denoting LC_{10} , LC_{15} , LC_{20} , LC_{25} , LC_{30} , and LC_{50} were calculated for further experiments.

2.6. Multigenerational sublethal effects of deltamethrin on biological traits and nutrient reserves of *C. cephalonica*

Regarding the feasibility of using *C. cephalonica* as a factitious host for rearing *H. hebetor*, the sublethal and low lethal effects of deltamethrin were studied. The effects of sublethal (LC_{10}), low lethal (LC_{15} , LC_{20} , LC_{25} and LC_{30}), and median lethal (LC_{50}) concentrations, along with control (Desneux et al., 2004, 2007; Ullah et al., 2019a, 2020), on the biological parameters and nutrient reserves of *C. cephalonica* were assessed for three consecutive generations (G0- parental generation; G1- first generation and G2- second generation). All the concentrations were administered along with a diet similar to the method mentioned above (section 2.5). One hundred third instar *C. cephalonica* larvae were released into Petri dishes containing the diet and the respective concentrations of deltamethrin and were designated the parental generation (G0). All Petri dishes were sealed with Parafilm to prevent insect escape. Treatment with sublethal concentrations continued until G1 and G2. Thirty surviving and healthy larvae were only considered for observations. Each larva was used as a single replication. The duration of development (hatching to adult emergence), larval weight gain (larval weight before pupation - larval weight before introduction in treatment), and fecundity (eggs laid/female) were recorded for each treatment and control. Individual larvae were weighed by placing them on a precision electronic balance ($\pm 1 \text{ mg}$, CY 223, Aczet Pvt. Ltd., Bangkok, Thailand). Similar observations were also recorded for the subsequent two generations (G1 and G2). Nutrient reserves of *C. cephalonica*, such as total midgut protein and total lipids, were estimated for all three

generations (G0, G1, and G2), and the methods followed are described below.

2.6.1. Protein estimation

Larval homogenates were prepared according to Macedo et al. (1993). Briefly, ten fifth instar larvae from the respective sublethal treatments in each generation were selected. These larvae were cold-immobilized and dissected under cold 250 mM NaCl and homogenized in cold distilled water (0.5 mL). There were three replications per treatment. The homogenate was centrifuged at $13,000 \text{ rpm}$ for 20 min at 4 °C. The supernatant was collected in a known volume of buffer (1 mL of 0.1 M Tris -buffer, pH 8.0). The protein concentration of the extracts was determined according to Lowry's methods with bovine serum albumin (BSA) as the standard (Lowry et al., 1951).

2.6.2. Lipid estimation

Total lipids were estimated as per the methodology described by Handel (1985). Ten- and fifth-instar larvae were placed into a clean glass tube and crushed with a glass rod in approximately 0.5 mL of chloroform–methanol (1:1). There were three replications per treatment. The tube was gently shaken, and then the supernatant was carefully transferred to another clean tube. Tubes were placed in a heating block to evaporate the solvent. Then, 0.2 mL of sulfuric acid was added and heated for 10 min. After cooling, vanillin reagent (5 mL) was added and allowed to develop a reddish color. The color is stable from 5 to 30 min and then slowly fades. The tubes were read at 525 nm absorbance against vanillin reagent as a blank.

2.7. Performance of *H. hebetor* on multigenerational sublethal concentration-treated *C. cephalonica*

Habrobracon hebetor females (<24 h post-eclosion) were paired with males for 24 h in a plastic container (500 mL) separately for mating. It was once observed that more than 80% of *H. hebetor* virgin females mate within the first 15 min (Ode et al., 1995). After 24 h of pairing, individual mated females were introduced (Ghimire and Phillips, 2014; Chen et al., 2011) into plastic containers containing G2 host larvae treated at sublethal concentrations [five host larvae of 4th instar (19–22 days) for each female *H. hebetor*] for 48 h as described earlier (Section 2.3). Twelve replications were maintained per treatment. After parasitization of host larvae, eggs were counted at $40\times$ magnification under a trinocular microscope (Nikon SMZ-745T), and fecundity (eggs laid/female) was recorded. Additionally, observations of larval hatch rate (%), pupation (%), sex-wise emergence (%) and longevity (days) were recorded.

2.8. Statistical analysis

Mortality data of *C. cephalonica* larvae were used to calculate median lethal (LC_{50}), low lethal (LC_{15} , LC_{20} , LC_{25} , and LC_{30}), and sublethal (LC_{10}) concentrations using probit analysis in PoloPlus® software (California, USA) with 95% fiducial limits. Shapiro-Wilk's test ($P > 0.05$) (Razali and Wah, 2011; Qu et al., 2020) and visual inspection of their histograms, normal Q-Q plots and box plots showed that the *C. cephalonica* data were normally distributed. However, *H. hebetor* data were not normally distributed; hence, transformations (arc sine or square root) were conducted before the data were subjected to one-way ANOVA. Two-way ANOVA was carried out to determine the effects of sublethal concentrations across generations in *C. cephalonica* (Qu et al., 2020). All the data points are the mean \pm standard deviation (SD). All analyses were conducted using SPSS 19.0 software, and treatment means were compared based on Tukey's honestly significant difference (HSD) test.

3. Results

3.1. Determination of the median lethal concentration (LC₅₀)

The linear regression of the concentration–mortality relationship fitted to the observed data ($\chi^2 = 0.95$, $df = 4$, $P = 0.384$) and thus was considered as valid, and the LC₅₀ of deltamethrin was 281.13 mg L⁻¹ for 48 h of exposure. Furthermore, sublethal concentrations of LC₁₀ (45.17 mg L⁻¹), LC₁₅ (64.08 mg L⁻¹), LC₂₀ (84.61 mg L⁻¹), LC₂₅ (107.40 mg L⁻¹), and LC₃₀ (133.04 mg L⁻¹) Supplementary Table 1 along with LC₅₀ and the control were selected to study their effects on demographic parameters in a factitious host, *C. cephalonica*, for three generations (Supplementary Table 1).

3.2. Multigenerational sublethal effects of deltamethrin on biological traits and nutrient reserves of *C. cephalonica*

In parental (G0) and subsequent generations (G1 and G2), the sublethal effects of deltamethrin on fecundity, developmental duration, larval weight gain, and larval nutrient reserves, viz., the protein and lipid contents of *C. cephalonica*, were determined (Table 1). Exposure to sublethal concentrations of deltamethrin had significant effects on *C. cephalonica* fecundity in the first (G1) ($F_{6, 208} = 5.93$; $P = 0.0044$) and second (G2) ($F_{6, 208} = 16.49$; $P < 0.0001$) generations but was not significant in the parental generation (G0) ($F_{6, 208} = 2.65$; $P = 0.337$). All sublethal concentrations did not significantly influence the duration of development of *C. cephalonica* compared to the control during G0 ($F_{6, 208} = 0.71$; $P = 0.6438$) and G1 ($F_{6, 208} = 1.23$; $P = 0.3551$), whereas at G2, the LC₁₅ treatment had a significantly lower developmental duration than all other treatments ($F_{6, 208} = 4.95$; $P = 0.009$). Larval weight gain is an important parameter predicting larval health. Treatments resulted in a non-significant gain in larval weight at G0 ($F_{6, 208} = 0.48$; $P = 0.809$), whereas during G1 and G2, treatments varied significantly, and the LC₁₅ treatment had the highest weight gains in larvae, i.e., 141 mg during G1 ($F_{6, 208} = 13.05$; $P < 0.0001$) and 163 mg during G2 ($F_{6, 208} = 9.28$; $P = 0.0006$), compared to all other treatments (Table 1).

There were non-significant differences among different sublethal treatments concerning total protein in G0. In G1 and G2, the LC₁₅ treatment had the highest total protein compared to all other treatments (G1: $F_{6, 208} = 130.30$; $P < 0.0001$ and G2: $F_{6, 208} = 184.40$; $P < 0.0001$). However, the total lipid content was highest in the LC₁₅ treatment in all three generations (G0: $F_{6, 208} = 155.60$; $P < 0.0001$, G1: $F_{6, 208} = 389.99$; $P < 0.0001$ and G2: $F_{6, 208} = 503.25$; $P < 0.0001$) (Fig. 1). Two-

way analysis of variance results revealed that all sublethal treatments exposed over generations and their interaction significantly influenced fecundity, larval weight, and the protein and lipid contents but did not affect the developmental duration (Table 2).

3.3. Performance of *H. hebetor* on multigenerational sublethal concentration-treated *C. cephalonica*

The performance of the parasitoid *H. hebetor* on the multigenerational sublethal concentration-treated factitious host *C. cephalonica* in terms of fecundity, larval hatch rate, pupation rate, sex-wise emergence rate, and sex-wise longevity is shown in Fig. 2. A significant increase in parasitoid fecundity of 65.33% was found in host larvae treated with LC₁₅ compared to the control ($F_{6, 82} = 55.59$; $P < 0.0001$). However, non-significant differences were observed between the treatments and the control in terms of hatch rate (50–96.97%) ($F_{6, 82} = 1.22$; $P = 0.3571$), pupation rate (66.67–100%) ($F_{6, 82} = 0.48$; $P = 0.8064$), total emergence (33.33–100%) ($F_{6, 82} = 2.91$; $P = 0.0542$) and male sex emergence (33.33–92.13%) ($F_{6, 82} = 0.26$; $P = 0.073$). Conversely, female sex emergence of *H. hebetor* was significantly affected ($F_{6, 82} = 10.60$; $P < 0.0003$). Regarding sex-wise longevity, male longevity was non-significantly affected among the treatments (20.67–24.67 days) (male: $F_{6, 82} = 1.65$; $P = 0.2161$), whereas female longevity was significantly influenced (female: $F_{6, 82} = 14.11$; $P < 0.0001$).

4. Discussion

The present study demonstrated that deltamethrin can promote transgenerational developmental effects in the rice moth *C. cephalonica*, which may stimulate parasitoid *H. hebetor* performance. Our results showed that deltamethrin was highly toxic to *C. cephalonica*, with an LC₅₀ of 281.13 mg L⁻¹. Our toxicity findings for deltamethrin are consistent with the previously reported LC₅₀ value (300 mg L⁻¹) (Sharma et al., 2010). Insecticides exhibit various sublethal effects apart from their lethal effects on exposed organisms (Desneux et al., 2007; Ullah et al., 2019b). Many insecticides kill insects at higher concentrations, whereas at lower concentrations, they stimulate biological and physiological processes of organisms. This biphasic response phenomenon of high-dose inhibition and low-dose stimulation following exposure is termed ‘hormesis’ (Calabrese and Blain, 2005; Guedes et al., 2016). It is a biphasic phenomenon of dose–response and is characterized by ‘high-dose inhibition and low-dose stimulation’. Many organisms, including insects, develop an adaptive mechanism in stressful

Table 1

Biological traits of the factitious host *Corcyra cephalonica* following multi-generational exposure to sublethal concentrations of deltamethrin. NS – Non-significant. Mean ± standard deviations marked with different letters in the same column are significantly different. G0: Parental generation; G1: First generation; G2: Second generation. LC: lethal concentration.

Treatment concentrations	Fecundity (No.)			Developmental duration (days)			Larval weight gain (mg)		
	G0	G1	G2	G0	G1	G2	G0	G1	G2
LC ₁₀	88.67 ± 4.03	90.33 ± 5.39 ^{ab}	121.67 ± 3.61 ^b	40.67 ± 1.37	43.00 ± 0.89	39.00 ± 1.79 ^{ab}	99.33 ± 5.47	106.00 ± 4.10 ^b	118.00 ± 3.22 ^b
LC ₁₅	89.33 ± 8.59	104.33 ± 4.93 ^a	143.33 ± 6.28 ^a	40.33 ± 2.5	41.00 ± 0.89	37.67 ± 1.37 ^b	101.67 ± 4.50	141.00 ± 10.55 ^a	163.00 ± 18.48 ^a
LC ₂₀	84.67 ± 9.89	97.33 ± 4.10 ^{ab}	114.00 ± 5.24 ^b	40.00 ± 0.89	39.33 ± 1.37	41.67 ± 1.37 ^{ab}	98.00 ± 5.59	109.33 ± 5.47 ^b	130.00 ± 9.08 ^b
LC ₂₅	91.67 ± 7.45	84.00 ± 7.32 ^b	123.00 ± 5.58 ^b	42.67 ± 1.03	39.67 ± 2.73	43.00 ± 1.79 ^a	98.67 ± 1.37	102.33 ± 4.93 ^b	127.00 ± 3.22 ^b
LC ₃₀	92.67 ± 4.03	86.67 ± 5.37 ^b	115.00 ± 2.73 ^b	41.33 ± 2.25	40.33 ± 1.86	42.00 ± 0.89 ^{ab}	99.00 ± 7.80	106.67 ± 4.23 ^b	128.67 ± 5.39 ^b
LC ₅₀	79.00 ± 2.37	89.33 ± 8.31 ^b	111.67 ± 1.86 ^b	40.67 ± 2.07	40.67 ± 1.86	38.67 ± 1.37 ^{ab}	94.67 ± 2.25	108.67 ± 4.03 ^b	123.33 ± 5.75 ^b
Control	89.67 ± 5.47	94.33 ± 5.59 ^{ab}	91.00 ± 2.73 ^c	40.00 ± 0.89	40.33 ± 1.87	42.00 ± 1.79 ^{ab}	100.33 ± 1.86	103.67 ± 1.37 ^b	107.33 ± 1.03 ^b
P value	0.337	0.0044	<0.0001	0.6438	0.3551	0.0090	0.8098	<0.0001	0.0006
F value	2.65	5.93	16.49	0.71	1.23	4.95	0.48	13.05	9.28
Tukey HSD at 5%	NS	14.066	19.066	NS	NS	4.6035	NS	18.384	28.025

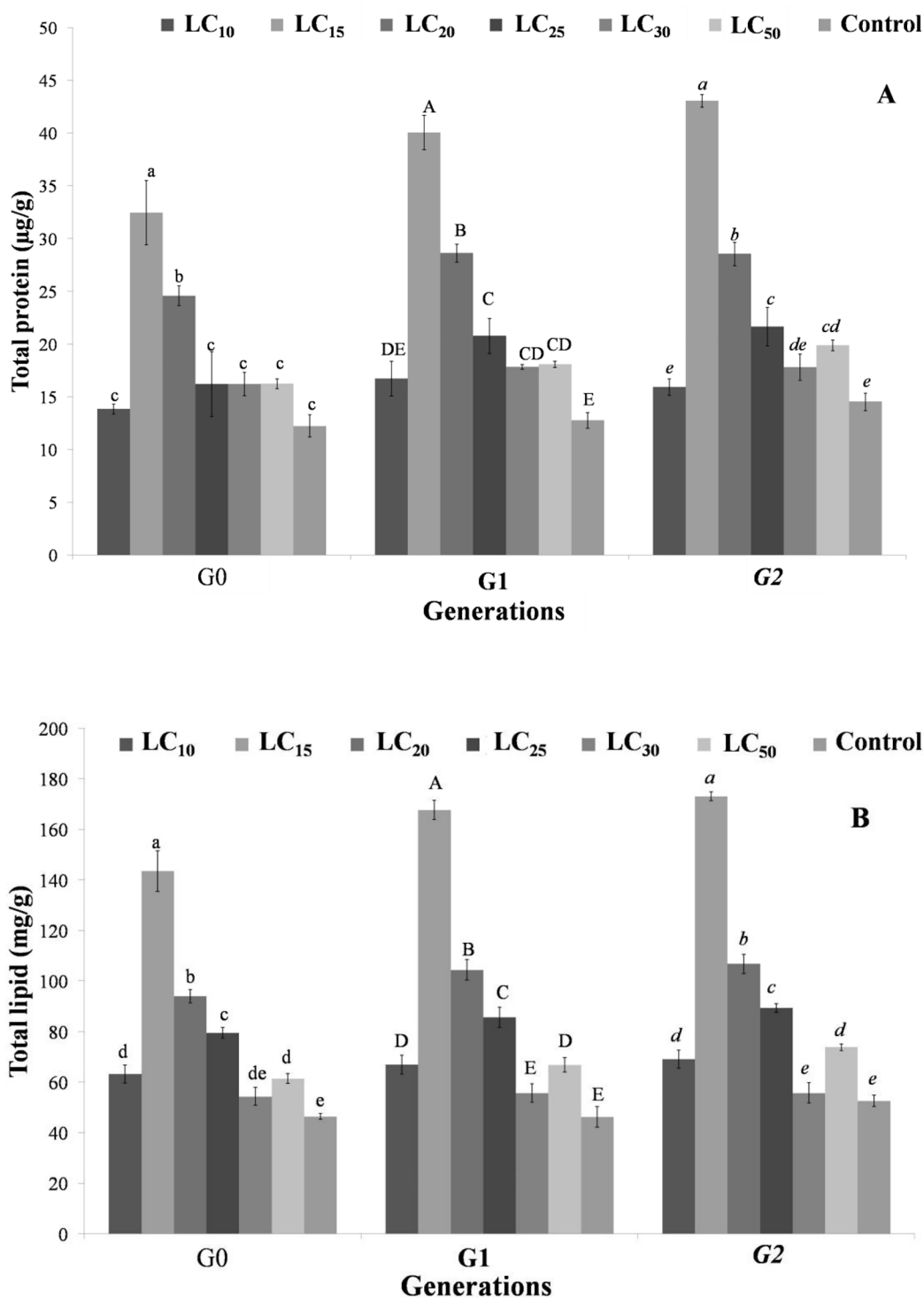


Fig. 1. Nutrient reserves, total protein (A) and total lipid (B) contents of the factitious host *Corcyra cephalonica* following multi-generational exposure to sublethal concentrations of deltamethrin. The same letters above error bars in each generation indicate no significant difference according to one-way ANOVA ($P < 0.05$). LC: Lethal concentration. G0: Parental generation; G1: First generation; G2: Second generation.

surroundings through their physiology and behavior (Sarfraz and Keddie, 2005; Cohen, 2006; Kanzaki and Tanaka, 2010). The study of insecticide-induced hormesis in insects has become an important area due to its potential implications in pest management (Morse, 1998; Sarfraz and Keddie, 2005; Cutler et al., 2009; Guedes et al., 2009; Ayyanath et al., 2013; Guedes and Cutler, 2014).

Previously, several authors have reported insecticide-induced multi-generational hormesis, such as our studies in many pest insects,

including *Myzus persicae* (Hemiptera: Aphididae) (Cutler et al., 2009; Tang et al., 2015; Zeng et al., 2016; Sial et al., 2018), *Aphis gossypii* (Hemiptera: Aphididae) (Wang et al., 2017; Ullah et al., 2020), citrus plant thrips (Morse and Zareh, 1991), and brown planthopper (Bao et al., 2009). All these studies were conducted directly on the target insects. However, in the current study, we recorded the host-mediated stimulation of parasitoids (indirect). In non-insects, host-mediated hormesis was reported in a copepod. Polycyclic aromatic hydrocarbon

Table 2

Two-way ANOVA results for multi-generational exposure examining the effects of deltamethrin sublethal concentrations on the factitious host *C. cephalonica*. *** - $P < 0.001$; ** - $P < 0.01$, * - $P < 0.05$, NS – Non-significant. G0: Parental generation; G1: First generation; G2: Second generation.

Parameter	Treatment (LC ₁₀ , LC ₁₅ , LC ₂₀ , LC ₂₅ and LC ₃₀)			Generation (G0, G1 and G2)			Treatment × Generation		
	F value	P value	Significance	F value	P value	Significance	F value	P value	Significance
Fecundity	7.9096	0.0013	***	150.8331	<0.0001	***	7.9259	<0.0001	***
Developmental duration	1.3913	0.2943	NS	0.1024	0.9030	NS	2.3106	0.0333	*
Larval weight	34.2617	<0.0001	***	69.8344	<0.0001	***	3.7143	0.0021	**
Protein	126.7799	<0.0001	***	84.6621	<0.0001	***	6.9377	<0.0001	***
Lipid	1626.9188	<0.0001	***	36.2598	<0.0001	***	4.1752	0.0009	***

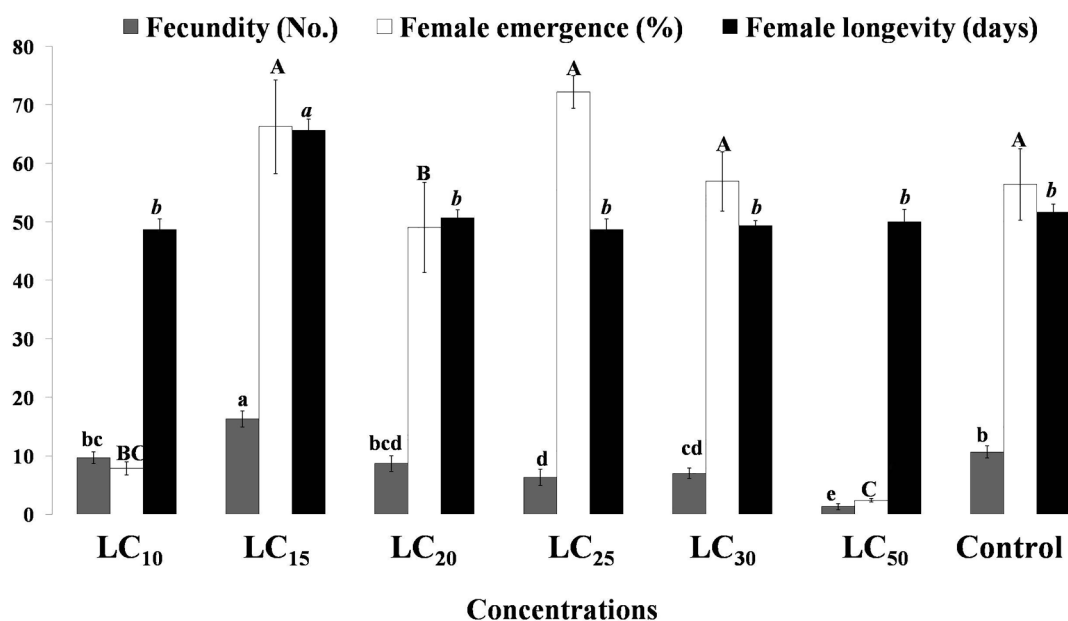


Fig. 2. Biological traits of the parasitoid *H. hebetor* following its development on a multi-generational sublethal concentration-exposed factitious host, *C. cephalonica*. The same letters above error bars in each generation indicate no significant difference according to one-way ANOVA ($P < 0.05$). LC: lethal concentration.

(PAH)-mediated changes in prey, the heterotrophic dinoflagellate *Oxyrrhis marina*, could have hormesis-like responses in copepod *O. davisae* (Saiz et al., 2009). Similar to our study but contrary to our results, host-mediated sublethal effects of the Cry1Ab protein on the parasitoid *C. marginiventris* through its host *S. frugiperda* were reported by Ramirez-Romero et al. (2007). Cry1Ab protein in Bt-maize tissue affected the developmental times, adult size, and fecundity of *C. marginiventris*. Moreover, Desneux et al. (2010) reported that frass odor was modified by Bt, and thus the parasitoids, *C. marginiventris* females, had a lower chance of detecting the host *S. frugiperda*. In the present study, sublethal concentrations of deltamethrin exposure to *C. cephalonica* did not show stimulatory or hormesis-like behavior in the parental generation (G0). However, in the descendant generations (G1 and G2), the effects were significant. Similar results were also reported by Ullah et al. (2020), who found that longevity and fecundity were reduced in the F₀ generation of *A. gossypii* upon LC₅ and LC₁₅ treatment with thiamethoxam. Several studies have reported similar results on insect pests following exposure to insecticides (Guo et al., 2013; Qu et al., 2015, 2017; Akhtar et al., 2021).

The application of sublethal concentrations of pyrethroids has shown effects on the developmental parameters of insects (Kerns and Stewart, 2000). In the present study, the sublethal effects of deltamethrin on the factitious host *C. cephalonica* were not dependent on concentration. Similar to our observations, it has been well established that sublethal exposure may induce many physiological effects, such as longevity and fecundity (Zhang et al., 2015; Santos et al., 2016). Fecundity of the host, developmental duration, larval weight gain, and protein and lipid contents increased after sublethal insecticide exposure in the current study.

Among all sublethal concentrations, LC₁₅ had the highest fecundity of *C. cephalonica* in the G2 generation. It has also been observed that stimulated growth, fecundity, and related responses are seen as inverted U-shaped curves (Cutler and Guedes, 2017). Hence, in our study, it is possible that LC₁₀ had lower stimulation followed by increased stimulation at LC₁₅, with further declines at LC₂₀, LC₂₅, LC₃₀, and LC₅₀, similar to an inverted U-shaped curve that indicates increased normal function at certain low doses (e.g., stimulated growth, fecundity). Our results on increased stimulation of *H. hebetor* at low lethal exposure (LC₁₅) partly corroborate the findings of Sial et al. (2018), who reported that low lethal exposure (LC₂₀) of acetamiprid significantly increased total fecundity, development time, and female longevity compared to the control in *M. persicae*.

However, in our study, there were no apparent stimulatory effects (hormesis) on different biological parameters in the parental generation (G0), though the effects were evident in later generations (G2). Concurrent findings were also observed in *A. gossypii* when exposed to imidacloprid (LC₂₀) (Shi et al., 2011; Chen et al., 2016). In *M. persicae*, there was no inhibition of longevity or developmental duration in the first two generations for hormetic concentrations, though inhibition was observed in later generations. This could be better explained by possible trade-offs through phenotypic or physiological characteristics in initial generations (Ayyanath et al., 2013).

Proteins are among the key biochemical constituents and are necessary for an organism to develop and accomplish its important activities. Proteins are essential for the individual-level fitness of insects and are associated with fecundity, growth rate, and body size. At higher community levels, proteins have been linked to population dynamics

and life histories of insects (Fagan et al., 2002). Our results showed a higher protein content at LC₁₅ than at other deltamethrin concentrations. Similar results were also obtained by Ismail (2020), who found increased protein content at the LC₂₅ of cyfluthrin (a pyrethroid). Piri et al. (2014) also found higher protein contents in *Glyphodes pyloalis* (Lepidoptera: Crambidae) at the LC₁₀, LC₂₀, LC₃₀, and LC₄₀ values of spinosad. Our results also specified that the protein contents in later generations (G1 and G2) were promoted compared with those in G0, which was in accordance with Chen et al. (2020), who reported that the protein contents of vitellogenin (Vg) and its receptor (VgR) were significantly higher in later generations compared to earlier generations in *Sogatella furcifera* (Hemiptera: Delphacidae) under the influence of an insecticide, triflumezopyrim. Additionally, a decrease in the total protein contents of silkworm larvae was also found due to sublethal concentrations of organophosphorus insecticides (Nath et al., 1997; Nath, 2003), which contradicts our results. Total protein is an essential biochemical factor for an organism to perform its biological activities. The increased protein in host larvae under sublethal concentrations could be explained in two possible ways: i) applied insecticide may inhibit the gene expression or may switch on other genes to synthesize mRNAs, which are subsequently translated into stress-induced proteins as an adaptation strategy to survive in the pesticide stress environment (Frigo et al., 2004; Ksenia et al., 2008); or ii) the increase in energy reserves such as proteins could be due to increased energy uptake from the environment (host diet in our study) when resources are not limited.

Insects can convert carbohydrates into lipids or can synthesize lipids and accumulate them in fat body tissue (Nation, 2001). Offspring whose mothers were exposed to insecticide are expected to be heavier and to accumulate more lipids than unexposed mothers (Margus et al., 2019). The current study showed a significant increase in total lipid contents at LC₁₅ and decreased levels at the remaining concentrations. Similar results were also noted by Piri et al. (2014), who reported higher lipid contents in larvae of *Glyphodes pyloalis* (Lepidoptera: Pyralidae) at LC₁₀ and lower lipid contents at the LC₂₀, LC₃₀, and LC₄₀ values of spinosad. Our results partly corroborate Ali et al. (2014), who found that increased total lipid contents were recorded in resistant beetles, *Rhyzopertha dominica*, treated with deltamethrin at sublethal concentrations. Conversely, the sublethal effects of cyantraniliprole reduced nutritional reserves such as carbohydrate, lipid, and protein contents, affecting larval development in *Agrotis ipsilon* (Lepidoptera: Noctuidae) (Xu et al., 2016) and in *Bradysia odoriphaga* (Diptera: Sciaridae) treated with benzothiazole (Zhao et al., 2016). The increased protein and lipid contents of the host can have beneficial effects in terms of parasitoid development (Barrett and Schmidt, 1991; Farahani et al., 2016a, 2016b); similar results were also obtained in the current study.

In the current study, fecundity, emergence, and female longevity in *H. hebetor* significantly differed when reared on sublethal deltamethrin-treated factitious hosts for three generations. Our results agreed with Asadi et al. (2018a), who showed that the percentage of parasitism (in our study revealed through fecundity) decreased with increasing sublethal concentration of malathion. Fecundity and mean longevity were reduced after direct adult exposure to sublethal concentrations (LC₃₀) of cypermethrin, NeemGuard, and BioNeem, but not the sex ratio, contradicting our results (Abedi et al., 2014). In both of these studies, the authors applied sublethal concentrations of insecticides directly to the parasitoid for a single generation, unlike our study; we first confirmed hormesis in the host insect after multi-generational insecticide treatment that subsequently improved performance in the parasitoid. Hormesis in insects is an example of homeostatic modulation (Cohen, 2006). Similar to our study, hormesis has also been reported in another host insect, *Galleria mellonella* (Lepidoptera: Pyralidae), due to mild heat shock, which in turn decreased its susceptibility to various entomopathogens, possibly due to enhanced antimicrobial peptides and lysozymes (Wojda et al., 2009).

Our results suggested that sublethal concentrations of deltamethrin on the host, *C. cephalonica*, could have stimulatory effects on *H. hebetor*

fecundity, emergence, and longevity, affirming the desired qualities of the parasitoid when reared without a major trade-off. This strategy could reduce both the application frequency and the total number of parasitoids used in biological control due to their enhanced performance. Rix and Cutler (2020) also observed that trade-offs due to insecticide-induced stimulations might have neutral or negative fitness effects on organisms. However, these trade-offs will not underlie hormetic effects. In contrast, stimulation of many traits without trade-offs is also possible within the same generation due to low insecticide concentrations (Zanuncio et al., 2005; Pereira et al., 2009). Ullah et al. (2020) reported hormesis effects of thiamethoxam on F₁ *A. gossypii*, which might be due to intermittent changes in the expression of genes involved in fertility, growth and insecticide detoxification. Moreover, several other studies have shown insecticide-induced hormesis effects on insects (Ayyanath et al., 2013; Guedes et al., 2016; Tang et al., 2019; Qu et al., 2020). Stimulatory effects in *A. gossypii* have been observed for sublethal concentrations of imidacloprid and acetamiprid (Ullah et al., 2019a, 2019b). Similar effects were examined in *Aphis glycines* Matsuura (Hemiptera: Aphididae) when they were exposed to sublethal concentrations of imidacloprid and beta-cypermethrin (Qu et al., 2015, 2017).

To conclude, our study demonstrates for the first time that insecticide hormesis in the host insect *C. cephalonica* at LC₁₅ could be exploited for quality mass rearing of *H. hebetor*, assuming that the stimulations are stable and heritable. Hence, maximum benefit can be obtained per unit of resources in terms of mass rearing of parasitoids compared to conventional rearing. Hormesis induced by sublethal and low lethal concentrations of insecticides was exploited in the current study for *C. cephalonica*, which is generally used to mass rear *H. hebetor*. The sublethal effects of insecticides were considered in a different approach to harness their benefits. However, long-term experiments are required to determine whether these stimulations could translate into economic benefits during mass culturing of beneficial insects and to understand any trade-offs that do occur. We propose additional research to confirm whether the trends hold across several generations. Additionally, apart from reproductive traits, other important characteristics for natural enemy success, such as the ability to withstand environmental factors and immunity against pathogens and parasites, may be validated across generations.

CRedit authorship contribution statement

G. Basana Gowda: Conceptualization, Funding acquisition, Writing - original draft. **Madhusmita Sahu:** Methodology, Investigation. **Farman Ullah:** Writing - review & editing. **Naveenkumar B. Patil:** Validation. **Guru Pirasanna Pandi:** Data curation. **Totan Adak:** Validation, Visualization. **Somnath Pokhare:** Software. **Annamalai Mahendiran:** Writing - review & editing. **Prakash Chandra Rath:** Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2021.104680>.

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