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RESEARCH ARTICLE

Transgenerational toxicity of imidacloprid on demography and behaviour of key larval parasitoid, *Habrobracon hebetor* (Say)

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Abstract

A successful Integrated Pest Management (IPM) program depends on using both bio agents and chemical pesticides, making it essential to consider pesticide effects on non-target organisms used in biological control. This study examines the effects of LC_5, LC_{30} and LC_{50} concentrations of imidacloprid on the demographic and behavioural traits of *Habrobracon hebetor* (Say) across successive generations (F_1 to F_5). In the bioassay experiments, imidacloprid exhibited profound toxicity, with an LC_{50} of 40.75 mg L^{-1}, while LC_5 was 0.27 mg L^{-1} and LC_{30} was 8.27 mg L^{-1}. Notably, egg and larval development periods were significantly prolonged in F5 individuals exposed to LC_5 and LC_{30} compared to those in F1. Key population parameters, including the net reproductive rate (R_0), gross reproductive rate (GRR) and mean generation time (T), were markedly lower in the F_5 generation, particularly at LC_{30}. Exposure to LC_{50} in the F5 generation resulted in extended egg, larval and pupal development durations, alongside reduced male longevity, fecundity and oviposition periods. All population parameters, except the intrinsic rate of increase (r) and finite rate of increase (λ), were significantly impacted. Additionally, walking behaviour differed significantly among individuals treated with LC_5, LC_{30} and LC_{50} concentrations; while LC_5 exposure notably increased walking speed, it still exerted a detrimental effect on demographic parameters overall. To minimize these adverse outcomes, optimizing the timing of pesticide application is essential to avoid antagonistic interactions with natural enemies in IPM programs.

Keywords: biological control; life table; mass rearing; natural enemy; sublethal

Introduction

The use of pesticides remains a cost-effective and convenient strategy for pest control, demonstrating high efficacy (1). However, injudicious pesticide usage has resulted in problems such as pest resistance, environmental pollution and crop residues risking human health (1). Insecticides may permeate the insect body directly through direct application, ingestion of treated food, or through contact of insects with residual substances (2). The impact of pesticides on both target and non-target insect populations is significantly influenced by the application rate (3). Beyond causing lethality, pesticides also trigger sublethal effects in treated organisms (4). These sublethal effects encompass a range of demographic and behavioural characteristics, including alterations in fecundity, developmental rate, sex ratio as well as variations in diapause behaviour and morphological changes, all of which significantly influence the growth of arthropod populations.

Habrobracon hebetor (Say) (Hymenoptera: Braconidae) is a gregarious, idiobiont larval ectoparasitoid of Lepidopteran insects (5). It is distinguished by its short generation time, high reproductive rate and versatility in adapting to different host species. *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) serves as a prominent host, particularly in the mass rearing of *H. hebetor.*

The success of an IPM program hinges on the effective integration of both chemical and biological control methods. A critical prerequisite for initiating a biological control program is a thorough evaluation of the lethal and sublethal effects of insecticides on non-target organisms (6). Exploration of these insecticidal effects can be conducted through various methodological approaches encompassing field studies, semi-field experiments, as well as laboratory investigations (7). Assessing the impact of insecticide toxicity on non-target organisms under controlled conditions is essential for obtaining reliable findings. Laboratory toxicological studies, particularly methodologies like life

table response experiments, are crucial in understanding sublethal effects (8). This is crucial as sublethal effects have the potency to adversely affect the physiology and behaviour of beneficial organisms, thereby necessitating focused studies on population dynamics.

Imidacloprid , a widely employed pesticide globally, is utilized on crops either through direct plant application, seed treatment, or soil treatment (9). It plays a pivotal role in pest management by effectively targeting plant and leafhoppers, whiteflies, aphids, termites and thrips. However, its prolonged persistence and toxicity pose risks to non-target organisms (10). Given the increasing emphasis on biological control in IPM stratergies, understanding the sublethal effects of pesticides on natural enemies is crucial. Numerous studies have investigated the sublethal impacts of various pesticides on *Habrobracon hebetor*, revealing significant effects on key biological and demographic parameters, including longevity, fecundity, fertility, parasitism rate, developmental duration, sex ratio, intrinsic and finite rates of increase, as well as net and gross reproductive rates (11-14). Despite this, most existing research has been confined to a single-generation assessment. To bridge this knowledge gap, the present study examines the residual toxicity of imidacloprid on the demographic and behavioural parameters of *H. hebetor* over five consecutive generations (F_1 to F_5) following initial exposure in the F_0 generation.

Materials and Methods

Study environment

The current experiment was conducted in the Biocontrol Laboratory of the Crop Protection Division at ICAR-Central Rice Research Institute (CRRI), Cuttack, India (20.4537° N, 85.9338° E). The study was carried out under controlled environmental conditions, maintaining a temperature of 25 ± 1 °C, relative humidity of 70 ± 5 %, (measured using an HTC-1 digital thermo-hygrometer) and a photoperiod of 14 hr light and 10 hr dark.

Initial colonies of the host, *Corcyra cephalonica*

Initial colonies of the factitious host, *C. cephalonica* were acquired from the mass-rearing facility located at ICAR-CRRI, Cuttack, India. The host *C. cephalonica*, was mass-reared following previously established protocols as described in earlier studies (15, 16). The insect colony was maintained for over 10 generations prior to its use in subsequent experiments. For experimental purposes, fourth or fifth instar larvae emerging from eggs, all reared on the same day, were selected to ensure uniformity in developmental stage.

Rearing of the parasitoid, *Habrobracon hebetor*

The parasitoid *H. hebetor* was reared using the standardized methodology detailed in the study (17). Upon the emergence of the adult parasitoids, a pair was introduced into a 1000 mL plastic container and allowed to mate for 24 hr. Five larvae of *C. cephalonica* (4^{th} and 5^{th} instars) were positioned between two layers of fine muslin cloth and positioned over the opening of the container (using the sandwich method) ((15,18). Cotton swabs dipped in a honey solution (50%) were provided to the parasitoids as food (12). After 48 hr of parasitization, the parasitized *C. cephalonica* larvae were transferred to an insect growth chamber and maintained under controlled standard laboratory conditions for further development (25 ± 1 °C, 70 ± 5% and 14:10 L:D) (16). The parasitoid was continuously reared for 10 generations before being used in further experiments to eliminate any prior effects.

Insecticide

In this experiment, a 98% pure technical-grade formulation of imidacloprid (Sigma Aldrich, St. Louis, MI, USA) was used. Serial dilution of the insecticide was prepared using analytical-grade acetone to achieve the requisite concentrations for conducting contact toxicity studies. Acetone was used as the control due to its negligible effect on insect behaviour and mortality. For further experiments, fresh insecticide dilutions were used to avoid chemical decomposition.

Toxicity assay

The toxicity of imidacloprid to *H. hebetor* was conducted through a concentration-mortality bioassay. A dry film deposition assay was conducted to assess the toxicity of imidacloprid on *H. hebetor* (<24 hr old), following the standardized protocol (19). Preliminary bioassay studies were conducted to establish a suitable range of concentrations for subsequent experiments. Five different concentrations i.e., 10, 50, 100, 150 and 200 mg L^{-1} of imidacloprid were used to establish a concentration-mortality curve.

After the preparation of insecticide solutions, 1 mL solution of insecticide was applied inside the glass tubes (Borosil®; height × diameter, 19.0 cm × 3.6 cm), by covering the inner surface to ensure homogeneous deposition. The tubes were gently rotated until all visible droplets had evaporated, then they were left at room temperature for approximately 1 hr to facilitate complete solvent evaporation. About 60 newly emerged adult wasps (<24 hr old) were introduced in the glass tubes, supplied with a streak of honey as a food source. Muslin cloth was used to cover the openings of the tubes, facilitating air movement.

Subsequently, the tubes were placed in an insect growth chamber (model: JSPC-420C; JS Research Inc., Gongju, Republic of Korea) configured at 25 °C, 70 % RH, 14L:10D. Three replications (corresponding to three tubes), were employed for each insecticide concentration. Following 24 hr of exposure, adult wasps were transferred to a separate tube devoid of pesticides, containing a honey streak. Mortality was recorded by counting the number of deceased parasitoids and the percentage of mortality was calculated. Wasps that did not move after being probed were declared dead.

Risk assessment

The ecological risk of imidacloprid to *H. hebetor* was assessed using the risk quotient (RQ) method. The RQ value was determined by dividing the field-recommended application rates of imidacloprid by the LC_{50} value for *H. hebetor* obtained from laboratory studies (20).

Risk quotient	Category
<50	Harmless
50-2500	Slightly to moderately toxic
>2500	Dangerous

Life table experiments

Different concentrations of imidacloprid (LC_5, LC_{30}, LC_{50}), along with a control (acetone), were applied to the parental generation (F_0) of *H. hebetor*. The subsequent exposure consequences were observed in the successive untreated generations (F_1 and F_5). The demographic parameters of *H. hebetor* were evaluated using the previously described methodology under standard laboratory conditions (temp. 25 ± 1 °C, RH 70 ± 5% and 14 hr L:10 h D) (21).

The developmental duration of *H. hebetor* was examined at LC_5, LC_{30} and LC_{50} concentrations, in addition to the control (acetone). 1 mL of each prepared insecticide concentration was applied to the inner surface of glass tubes. The parental generation consisted of about 100 adult wasps (<24 hr old) per treatment group, which were exposed to the treated tubes. After 24 hr of exposure, the living insects were transferred to a pesticide-free 1000 mL plastic container and provided with late-instar larvae of *C. cephalonica*. Following adult emergence, about 80 pairs of parasitoids were transferred individually in small plastic boxes (height × diameter, 40 mm × 35 mm) and each pair was provided with one late-instar larva of *C. cephalonica* for parasitization (22). After 24 hr, the parasitized larvae were placed individually in Petri dishes (BR Biochem; height × diameter, 90 mm × 15 mm), ensuring that only a single egg remained per larva, with excess eggs carefully removed. Daily observations were conducted to monitor each developmental stage through to adult emergence and the sex of each emerging adult was recorded.

Fecundity and longevity assessments of *H. hebetor* adults were conducted in controlled environmental conditions (25 ± 1 °C, 70 ± 5% and 14:10 L:D). From the above developmental studies, thirty pairs of parasitoids (<24 hr old) were isolated in separate plastic boxes and supplied with a streak of honey. Daily, two fresh larvae of *C. cephalonica* were provided to each pair until the female wasp died naturally (21). The parasitized host larvae were extracted daily and subsequently incubated until offspring emerged. The longevity and fecundity of the adult, as well as the rate of emergence and sex ratio of the offspring, were documented for both untreated generations (F_1 and F_5) (23).

Behavioural experiment

The walking speed of the parasitoid *H. hebetor* was assessed at different concentrations of imidacloprid (LC_5, LC_{30}, LC_{50}), along with a control (acetone), following a standardized method (24). One treated female was randomly selected from each concentration group and individually transferred to a pesticide-free petri dish. A sheet of smooth white paper was placed to cover the base of the petri dish and a 1 cm reference line was drawn on the surface to standardize the speed measurements. A Nikon Z30 Digital camera was used to document the walking behaviour of individual wasps for 20 min. The original MP4 video footage was partitioned into four distinct 5-min segments, each regarded as a replication. The Kinovea software (v0.9.5; https://www.kinovea.org/), a video annotation tool equipped with object-tracking functionality, was employed to analyze these segments. Each segment was analyzed to detect a single, continuous movement lasting a minimum of 10 sec. Ultimately, all eligible movement segments were aggregated and averaged for each wasp, yielding a comprehensive understanding of their movement dynamics.

Statistical analysis

Mortality data were analysed using probit analysis using PoloPlus version 2.0 (LeOra Software Inc., Berkeley, CA, USA) to determine LC_5, LC_{30}, LC_{50} and LC_{90} values, along with corresponding 95% confidence intervals (25).

Life history data of *H. hebetor* reared on *C. cephalonica* larvae were analyzed using the age-stage, two-sex life table theory implemented in the TWOSEX-MSChart program (26). The bootstrap method, with 100000 resamples, was employed to calculate means, variances and standard errors of biological and population parameters (27). Statistical comparisons between imidacloprid-treated and control groups, as well as intergenerational differences within each treatment, were conducted using the paired bootstrap test. Walking speed data of *H. hebetor* were analyzed using one-way ANOVA to compare treatment and control groups within the F_1 and F_5 generations and paired t-tests were used to compare between generations within each treatment group. Tukey's multiple comparison test (P = 0.05) was applied using IBM® SPSS® Statistics Version 22.

Results

Toxicity of imidacloprid to *Habrobracon hebetor* adults

The imidacloprid concentrations for *H. hebetor* adults were determined through probit regression analysis. The derived regression equation for the dose-response relationship was $y = 0.7655x + 3.768$, with an R^2 value of 0.8348, demonstrating a strong correlation and a reliable fit to the observed data. The concentration-mortality assay resulted in LC_{50} value of 40.75 mg L^{-1} and an LC_{90} value of 2006.34 mg L^{-1},with corresponding 95% fiducial limits of 13.91-119.38 mg L^{-1} and 684.88-5877.52 mg L^{-1}, respectively (Table 1). Additionally, the LC_5 concentration was calculated as 0.27 mg L^{-1}, with a confidence interval of 0.09-0.80 mg L^{-1}, while the LC_{30} value was determined to be 8.27 mg L^{-1}, with a confidence interval of 2.82-24.24 mg L^{-1}(Table 1). The calculated risk quotient calculated was 0.61, which falls below the threshold of 50, indicating that imidacloprid poses a low level

Table 1: Toxicity of imidacloprid to the ecto-parasitoid, *H. hebetor*

Insecticide	*n*	Slope ± SE*	LC_5 mg L^{-1} (95% CL)	LC_{30} mg L^{-1} (95% CL)	LC_{50} mg L^{-1} (95% CL)	LC_{90} mg L^{-1} (95% CL)	X^2 (df)†
Imidacloprid	60	0.766 ± 0.238	0.27 (0.09-0.80)	8.27 (2.82-24.24)	40.75 (13.91-119.38)	2006.34 (684.88-5877.52)	0.831 (3)

*SE.

†Chi-square value (X^2) and degrees of freedom (df) as calculated by PoloPlus® software (California, USA); LC, lethal concentration; CL, Confidence limit.

of toxicity to *H. hebetor* (section 2.6). Subsequently, LC_5, LC_{30} and LC_{50} concentration, along with the control (acetone), were selected to evaluate the effect of imidacloprid on the biological, population and behavioural parameters of *H. hebetor* across five successive generations (F_1 to F_5).

Biological parameters of *Habrobracon hebetor* exposed to imidacloprid

The effects of imidacloprid on the biological parameters of the larval parasitoid *H. hebetor* in the F_1 and F_5 generations are documented in Table 2. The findings indicated that exposure to LC_5 led to a noteworthy difference in adult longevity and total longevity in the F_1 generation compared to the control group. In the F_5 generation, most biological parameters showed no significant difference under LC_{50} exposure, except for the developmental duration of the eggs and larval stages, which were notably different from the control. A generational comparison indicated a marked decline in fecundity ($p < 0.0001$), decreasing from 127.09 ± 9.95 in the F_1 generation to 61.42 ± 5.77 in F_5. Under LC_{30} exposure, significant decrease was noticed in female longevity, fecundity and oviposition days were observed in the F_5 generation compared to F_1 generation, whereas no such differences were observed in male longevity, total longevity and TPOP. In *H. hebetor* individuals of the F_5 generation, there was a noteworthy elevation in the developmental days of the egg by 10% ($p = 0.001$), male longevity by 13.4% ($p = 0.033$) and TPOP by 4.7% ($p = 0.0004$) when compared to the control group. However, a significant reduction in the larval developmental period from 1.72 ± 0.06 to 1.67 ± 0.07 and fecundity from 73.12 ± 6.46 to 56.29 ± 8.05 was noticed in the LC_{30}exposed F_5 individuals when compared to control. LC_{50} exposure to *H. hebetor* exhibited notable differences in biological parameters such as the developmental period of the eggs ($p = 0.023$), larvae ($p = 0.017$), pupae (p = 0.005) and fecundity ($p = 0.024$), when compared to the control during the F_5 generation. Furthermore, a substantial reduction in fecundity by 36.5%, was seen in the F_5 individuals subjected to LC_{50}, relative to the control group (Table 2).

Population parameters of *Habrobracon hebetor* exposed to imidacloprid

The impact of imidacloprid on the population parameters of the F_1 and F_5 generation of *H. hebetor* are provided in Table 3. Individuals exposed to the LC_5 concentration exhibited a significant reduction in the net reproductive rate (R_0) ($p = 0.024$), mean generation time (T) ($p = 0.026$) and gross reproductive rate (GRR) ($p = 0.001$) in the F_5 generation upon comparison with the F_1. However, no significant differences were observed in any population parameters between the LC_5-exposed individuals compared to the control. Exposure to LC_{30} concentration had no noteworthy variations in the population parameters compared to the control in both F_1 and F_5 generations. On the contrary, when comparing among generations, all population parameters, including r ($p = 0.013$), λ ($p = 0.012$), R_0 ($p = 0.002$), GRR ($p = 0.0003$) and T ($p = 0.011$) showed significant differences. *H. hebetor* adults exposed to LC_{50} concentration showed no significant variations from the control in both generations, except for the GRR ($P = 0.001$) of the F_1 generation.

Age-stage specific survival rate, fecundity and life expectancy of imidacloprid exposed *H. hebetor*

The age-stage-specific survivorship curve (s_{xj}) denotes the likelihood of neonatal survival from age x to stage j, as depicted in Fig. 1. Notably, owing to variations in developmental durations, there is discernible overlap among different stages (Fig. 1). The discernible trend reveals a gradual reduction in survival rates during the transition from immature to adult stages. The age-specific survival rate (l_x), age-specific fecundity of the total population (m_x) and age-specific maternity (l_xm_x) for *H. hebetor* exposed to imidacloprid in F_1 and F_5 generations are illustrated in Fig. 2. The l_x curves, representing survival rates without stage distinction, exhibit a noteworthy decrease at 40 and 45 days for both F_1 and F_5 generations exposed to LC_5 and LC_{50} concentrations, respectively. For the LC_{30} concentrations, the decline occurs at 40 and 41 days (F_1 and F_5, respectively), contrasting with control groups where the declining trend halts at 43 and 40 days for F_1 and F_5generations, respectively (Fig. 2). The m_x and l_xm_x curve manifest a statistically significant decline earlier in the LC_5 and LC_{30} groups compared to the control, evident in both the F_1 and F_5 generations.

The age-stage-specific life expectancy (e_{xj}), which indicates the expected remaining lifespan of an individual at age x and stage j, as shown in Fig. 3. The curve suggests that individual exposure to LC_5 and LC_{30} survive longer than those exposed to LC_{50} group (Fig. 3). Notably, concerning the effect on F_1 and F_5 generations, the e_{xj} curve for F_5 adults tends to decline earlier than that of F_1 adults, indicating a transgenerational impact of the treatment. The age-stage-reproductive value (v_{xj}), characterizes the contribution of the population from age x to stage j to future offspring, as demonstrated in Fig. 4. A higher reproductive value trend is observed in the LC_5 and LC_{30} treatments compared to the LC_{50}, specifically in the F_5 generation (Fig. 4).

Walking behaviour of *H. hebetor* exposed to imidacloprid

The effect of imidacloprid on the walking speed of *H. hebetor* in the F_1 and F_5 generations is detailed in Fig. 5. The results demonstrate that, apart from the LC_{50} concentration, all treatments led to noticeable differences in walking speed across both generations. In the F_1 generation, the walking speed of individuals exposed to LC_{50} declined significantly compared to the control group. By the F_5 generation, significant reductions in walking speed were observed in individuals treated with LC_{30} and LC_{50} concentrations when compared to both the control and LC_5 treatments (Fig. 5). In the F_1 generation, reductions in walking speed of 10.5%, 49.6% and 33.3% were observed for individuals exposed to LC_5, LC_{30} and LC_{50} treatments, respectively, relative to the control. These reductions were higher in the F_5 generation, with declines of 16.3%, 16.9% and 53.1% for LC_5, LC_{30} and LC_{50} treatments, respectively. Interestingly, in the F_5 generation, walking speed in LC_5-treated individuals significantly increased, rising from 3.41 ± 0.10 to 4.00 ± 0.17. In contrast, individuals exposed to LC_{30} and LC_{50} concentrations exhibited reduced locomotor activity, with walking speeds decreasing from 3.12 ± 0.12 to 2.48 ± 0.11 and from 2.54 ± 0.16 to 2.30 ± 0.11, respectively (Fig. 5).

Table 2: Biological parameters of F1 and F5 generations of H. *hebetor* exposed to different concentrations of imidacloprid

Biological parameters	Generations	Mean ± SE*,†					
		Control	LC_5	Control	LC_{30}	Control	LC_{50}
Egg (days)	F_1	1.63 ± 0.07^{bA}	1.59 ± 0.07^{bA}	1.63 ± 0.07^{bA}	1.68 ± 0.07^{bA}	1.63 ± 0.07^{bA}	1.49 ± 0.07^{bA}
	F_5	2.00 ± 0.02^{aB}	2.19 ± 0.06^{aA}	2.00 ± 0.02^{aB}	2.20 ± 0.06^{aA}	2.00 ± 0.02^{aB}	2.10 ± 0.04^{aA}
Larva (days)	F_1	1.38 ± 0.07^{bA}	1.41 ± 0.07^{bA}	1.38 ± 0.07^{bA}	1.32 ± 0.07^{bA}	1.38 ± 0.07^{bA}	1.51 ± 0.07^{bA}
	F_5	1.72 ± 0.06^{aB}	1.63 ± 0.07^{aA}	1.72 ± 0.06^{aB}	1.67 ± 0.07^{aA}	1.72 ± 0.06^{aB}	1.90 ± 0.04^{aA}
Pupa (days)	F_1	5.00 ± 0.05^{aA}	5.00 ± 0.03^{aA}	5.00 ± 0.05^{aA}	5.00 ± 0.02^{aA}	5.00 ± 0.05^{aA}	5.00 ± 0.04^{aA}
	F_5	3.94 ± 0.08^{bA}	4.04 ± 0.08^{bA}	3.94 ± 0.08^{bA}	4.11 ± 0.06^{bA}	3.94 ± 0.08^{bA}	3.63 ± 0.07^{bB}
Female longevity (days)	F_1	28.05 ± 2.45^{aB}	34.50 ± 1.57^{aA}	28.05 ± 2.45^{aB}	35.81 ± 1.78^{aA}	28.05 ± 2.45^{aB}	34.96 ± 1.60^{aA}
	F_5	31.28 ± 1.13^{aA}	32.70 ± 1.20^{aA}	31.28 ± 1.13^{aA}	29.81 ± 1.48^{bA}	31.28 ± 1.13^{aA}	31.71 ± 1.50^{aA}
Male longevity (days)	F_1	13.07 ± 0.84^{bB}	16.90 ± 1.21^{aA}	13.07 ± 0.84^{bB}	18.93 ± 1.31^{aA}	13.07 ± 0.84^{bB}	20.08 ± 1.06^{aA}
	F_5	15.84 ± 0.52^{aA}	16.75 ± 0.53^{aA}	15.84 ± 0.52^{aB}	17.96 ± 0.85^{aA}	15.84 ± 0.52^{aA}	15.48 ± 0.53^{bA}
Total longevity (days)	F_1	15.97 ± 1.51^{bB}	21.37 ± 1.63^{aA}	15.97 ± 1.51^{bB}	22.52 ± 1.65^{aA}	15.97 ± 1.51^{bB}	22.77 ± 1.64^{aA}
	F_5	20.13 ± 1.44^{aA}	20.28 ± 1.56^{aA}	20.13 ± 1.44^{aA}	18.17 ± 1.49^{aA}	20.13 ± 1.44^{aA}	20.00 ± 1.50^{aA}
Fecundity	F_1	138.65 ± 16.11^{aA}	127.09 ± 9.95^{aA}	138.65 ± 16.11^{aA}	161.43 ± 11.18^{aA}	138.65 ± 16.11^{aA}	116.13 ± 9.66^{aA}
	F_5	73.12 ± 6.46^{bA}	61.42 ± 5.77^{bA}	73.12 ± 6.46^{bA}	56.29 ± 8.05^{bA}	73.12 ± 6.46^{bA}	53.54 ± 5.74^{bB}
TPOP (days)	F_1	8.00 ± 0.05^{aA}	8.00 ± 0.08^{aA}	8.00 ± 0.05^{aA}	8.00 ± 0.01^{aA}	8.00 ± 0.05^{aA}	8.00 ± 0.03^{aA}
	F_5	7.64 ± 0.10^{bA}	7.96 ± 0.04^{aA}	7.64 ± 0.10^{bB}	8.00 ± 0.85^{aA}	7.64 ± 0.10^{bA}	7.78 ± 0.11^{aA}
Oviposition days	F_1	13.70 ± 1.65^{aA}	14.09 ± 0.82^{aA}	13.70 ± 1.65^{aA}	17.25 ± 0.80^{aA}	13.70 ± 1.65^{aA}	14.65 ± 1.12^{aA}
	F_5	11.04 ± 0.83^{aA}	10.54 ± 0.77^{bA}	11.04 ± 0.83^{aA}	9.90 ± 1.05^{bA}	11.04 ± 0.83^{aA}	9.70 ± 0.71^{bA}

*Mean and Standard Errors (SE) were calculated using the bootstrap technique with 100,000 re-samples.

†Significant differences between generations and two treatments were estimated using the paired bootstrap test in the TWO-SEX MS Chart ($P < 0.05$).

Different lower-case letters indicate significant differences between F1 and F5 generations within each treatment group, while upper-case letters indicate significant differences between control and imidacloprid treatments in each generation. TPOP, total preoviposition period; LC, lethal concentration.

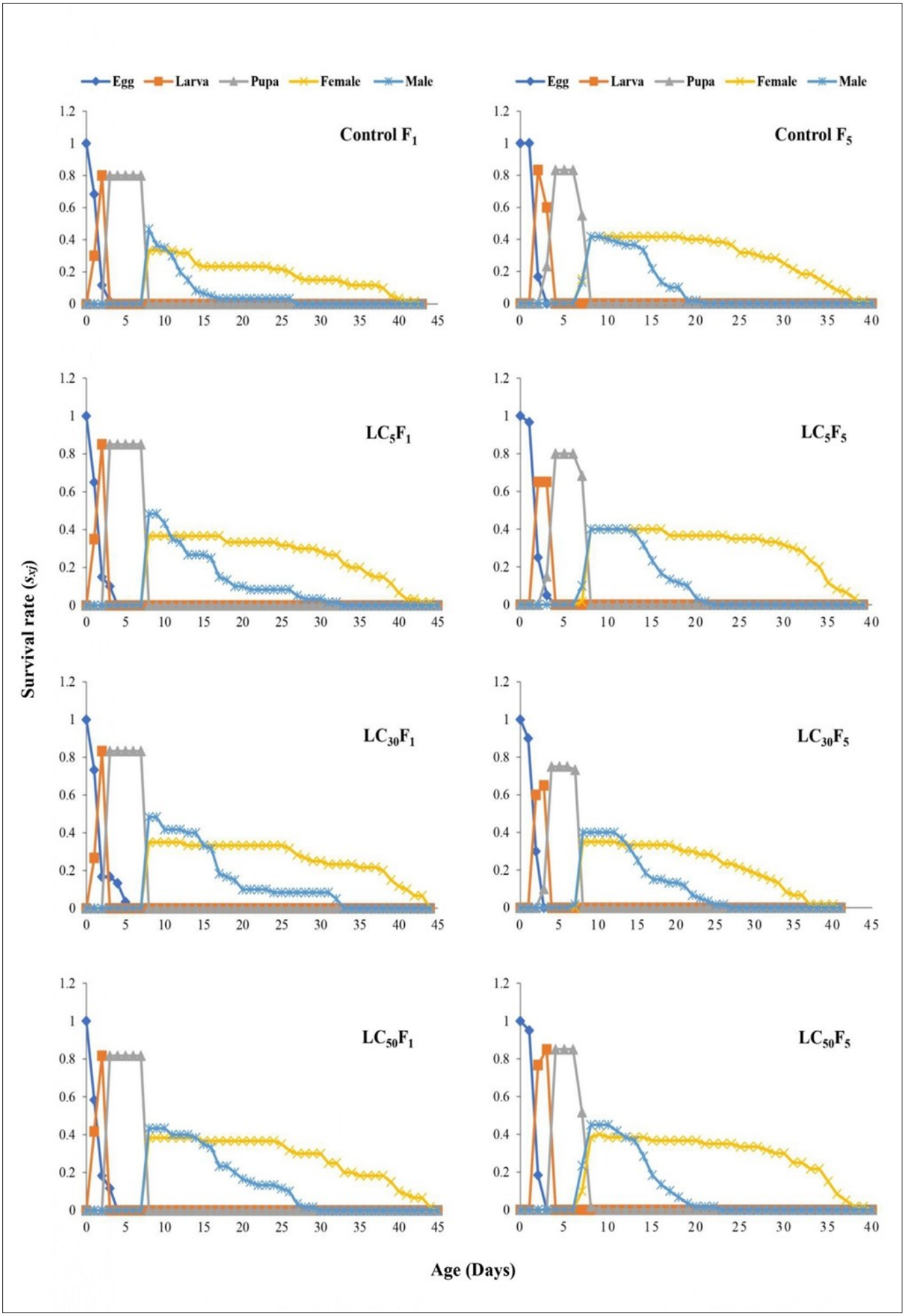

Fig. 1. Age–stage–specific survival rates (s_{xj}) of *H. hebetor* adults treated with acetone and LC_5, LC_{30} and LC_{50} concentrations of imidacloprid in F_1 and F_5 generations. These data were generated using TWO-SEX MS Chart.

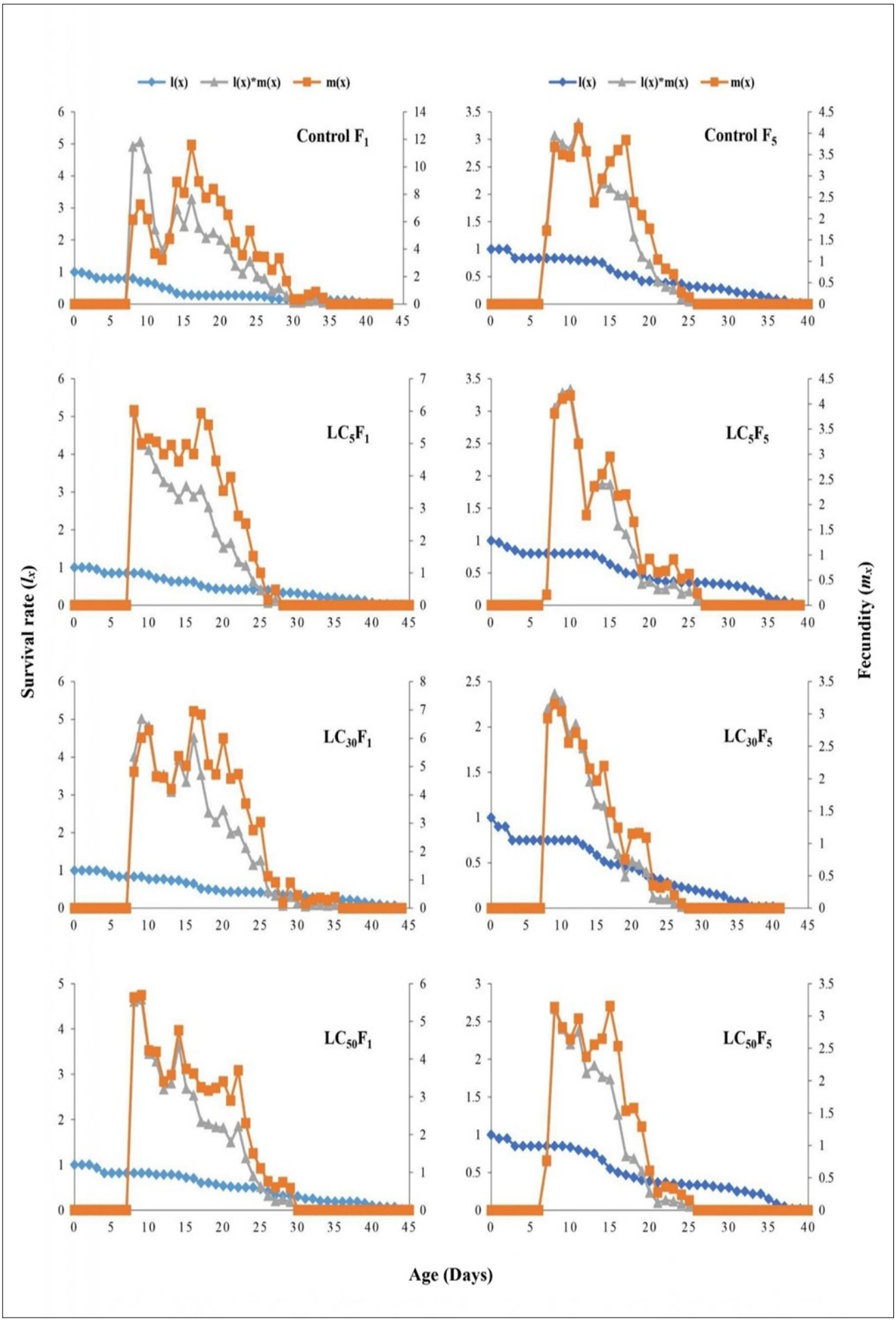

Fig. 2. Age-specific survival rate (l_x), age-specific fecundity of total population (m_x) and age-specific maternity ($l_x m_x$) of *H. hebetor* adults treated with acetone and imidacloprid in F_1 and F_5 generations. These data were generated using TWO-SEX MS Chart.

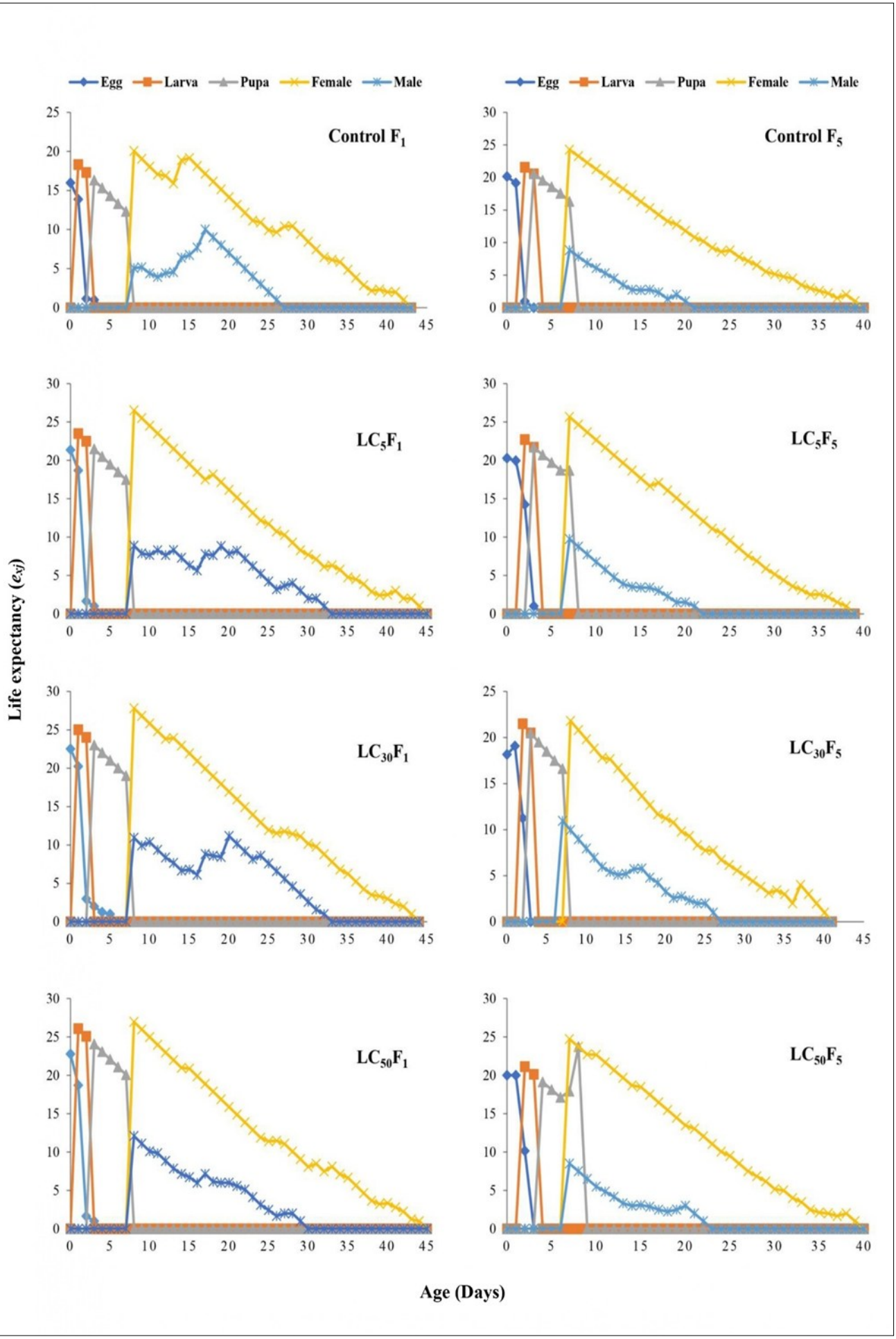

Fig. 3. Age-stage-specific life expectancy (e_{xj}) of *H. hebetor* adults treated with acetone and imidacloprid in F_1 and F_5 generations. These data were generated using TWO-SEX MS Chart.

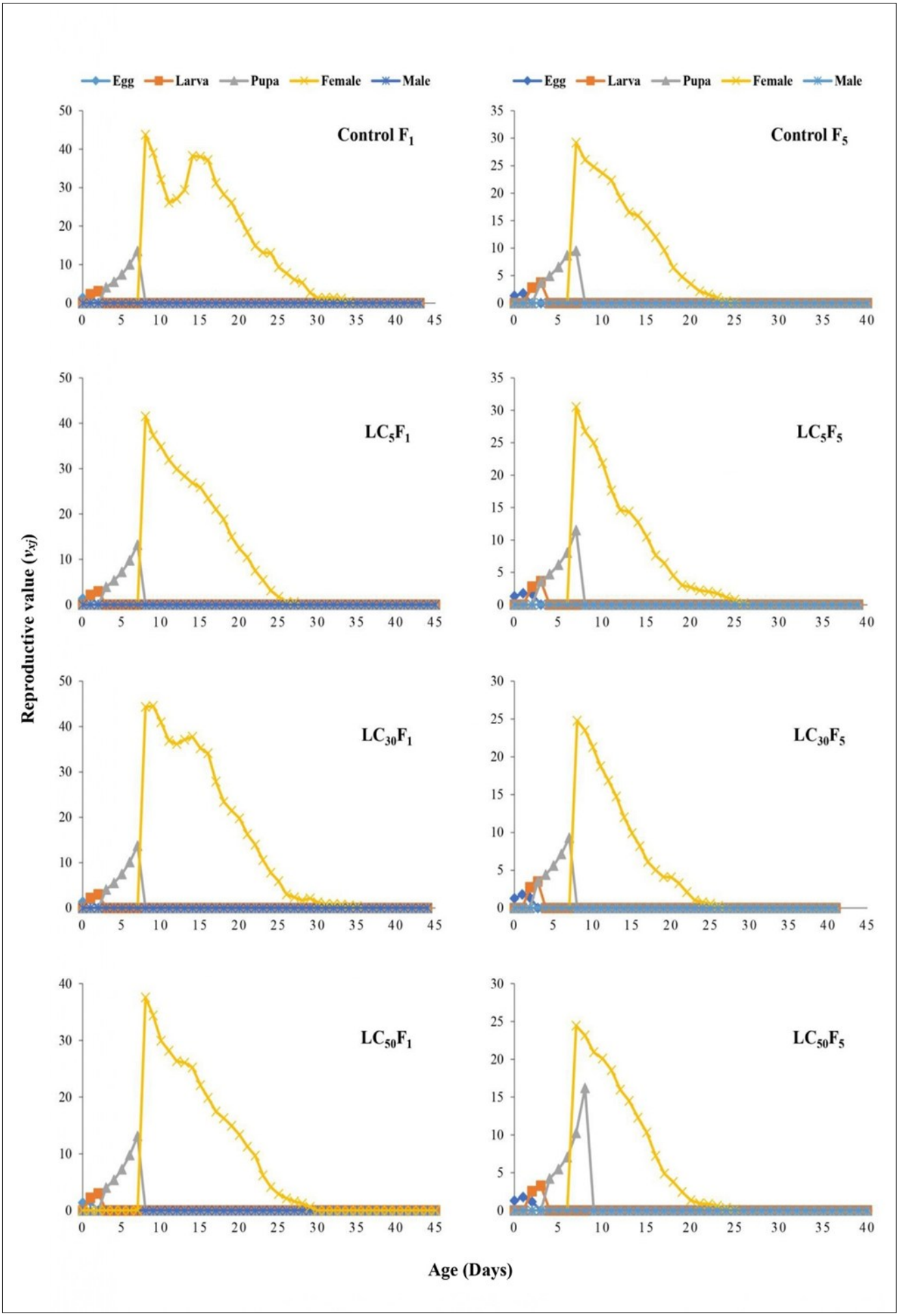

Fig. 4. Age-stage-reproductive value (v_{xj}) of *H. hebetor* adults treated with acetone and imidacloprid in F_1 and F_5 generations. These data were generated using TWO-SEX MS Chart.

Table 3: Population parameters of F_1 and F_5 generations of *H. hebetor* exposed to different concentrations of imidacloprid

Population parameters	Generations	Mean ± SE			
		Control	LC_5	LC_{30}	LC_{50}
***r* (d^{-1})**	F_1	0.30 ± 0.02^{aA}	0.30 ± 0.02^{aA}	0.30 ± 0.02^{aA}	0.30 ± 0.02^{aA}
	F_5	0.28 ± 0.02^{aA}	0.27 ± 0.02^{aA}	0.24 ± 0.02^{bA}	0.26 ± 0.02^{aA}
***λ* (d^{-1})**	F_1	1.35 ± 0.02^{aA}	1.35 ± 0.02^{aA}	1.36 ± 0.02^{aA}	1.34 ± 0.02^{aA}
	F_5	1.33 ± 0.02^{aA}	1.30 ± 0.02^{aA}	1.27 ± 0.02^{bA}	1.29 ± 0.02^{aA}
***R_0* (offspring/ individual)**	F_1	46.22 ± 9.97^{aA}	46.60 ± 8.67^{aA}	56.50 ± 10.66^{aA}	44.52 ± 8.16^{aA}
	F_5	30.47 ± 5.35^{aA}	24.57 ± 4.51^{bA}	19.70 ± 4.44^{bA}	21.42 ± 4.08^{bA}
***T* (days)**	F_1	12.88 ± 0.28^{aA}	12.70 ± 0.19^{aA}	13.25 ± 0.18^{aA}	12.81 ± 0.23^{aA}
	F_5	12.08 ± 0.24^{bA}	12.05 ± 0.22^{bA}	12.42 ± 0.27^{bA}	11.99 ± 0.32^{bA}
***GRR* (offspring/ individual)**	F_1	129.33 ± 15.63^{aA}	76.83 ± 10.96^{aB}	94.41 ± 13.41^{aA}	66.09 ± 10.24^{aB}
	F_5	45.37 ± 6.32^{bA}	36.49 ± 5.90^{bA}	31.41 ± 6.53^{bA}	31.95 ± 5.60^{bA}

*Mean and Standard Errors (SE) were calculated using the bootstrap technique with 100,000 re-samples.

†Significant differences between generations and two treatments were estimated using the paired bootstrap test in the TWO-SEX MS Chart ($P < 0.05$).

Different lower-case letters indicate significant differences between F1 and F5 generations within each treatment group, while upper-case letters indicate significant differences between control and imidacloprid treatments in each generation. *r*, intrinsic rate of increase; *λ*, finite rate of increase; *R0*, net reproductive rate; *T*, mean generation time; *GRR*, gross reproductive rate; LC, lethal concentration.

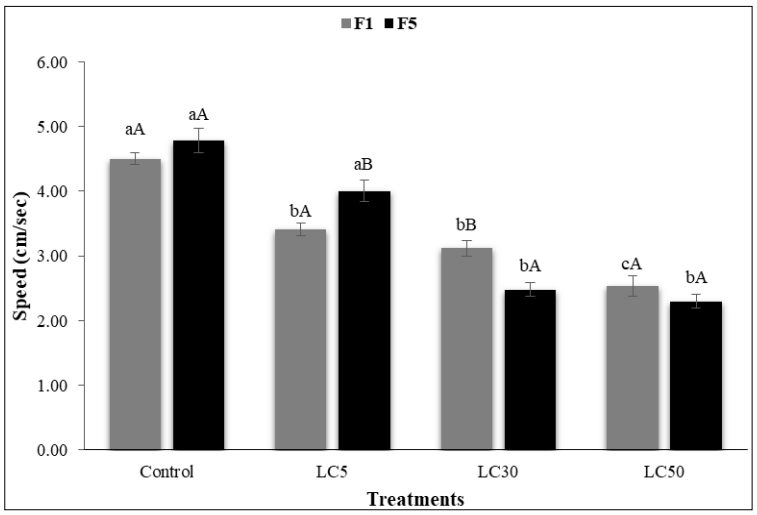

Fig. 5. Walking behaviour of *H. hebetor* adults treated with acetone and imidacloprid in F_1 and F_5 generations. Different lower-case letters indicate significant differences between control and imidacloprid treatments in each generation ($P < 0.05$, one-way ANOVA), while upper-case letters indicate significant differences between F_1 and F_5 generations within each treatment group ($P < 0.05$, paired T-test).

Discussion

In the realm of agricultural pest management, the widespread application of insecticides poses a significant risk to non-target organisms, including beneficial insects utilized in IPM programs. Understanding the impact of pesticides on biocontrol agents is crucial for the successful implementation of IPM strategies that integrate both biological and chemical control methods (28). Consequently, there is a necessity for toxicological investigations on the effects of chemical pesticides on natural enemies (28).

This study aims to elucidate the repercussions of imidacloprid exposure on the parasitoid *H. hebetor*. The findings reveal that imidacloprid exhibits high toxicity, with an LC_{50} value of 40.75 mg L^{-1}, which is consistent with previous research reporting an LC_{50} of 42.13 mg L^{-1} (29). In contrast, a lower LC_{50} value of 9.5 mg L^{-1} was reported for *Bracon brevicornis* (Wesmael) (Hymenoptera: Braconidae) (30). The field-recommended concentration (FRC) of imidacloprid (17.80% SL) is 25 g a.i./ha (31) and according to the risk quotient method (20), imidacloprid demonstrates low toxicity to *H. hebetor*. This outcome aligns with earlier studies, where imidacloprid was shown to have minimal adverse effects on *H. hebetor* (11, 32).

Beyond its lethal effects, chemical insecticides can elicit sublethal impacts that influence various physiological and behavioral traits in exposed arthropods (33, 34). These sublethal effects can be either beneficial or detrimental to insect populations (35). In this study, LC_5 (0.27 mg L^{-1}) and LC_{30} (8.27 mg L^{-1}) concentrations of imidacloprid significantly influenced developmental parameters-positively affecting the egg development period, while negatively impacting larval development. An accelerated developmental rate may be disadvantageous for parasitoids if it leads to desynchronization with the susceptible stages of their hosts (33). For instance, fenoxycarb has been reported to prolong the developmental duration of the predator *Chrysoperla rufilabris Burmeister* (Neuroptera: Chrysopidae) across all stages except the pupal stage, which corresponds with our observations (36). A previous study indicated that parasitoids exposed to buprofezin during later developmental stages exhibited reduced sensitivity compared to those treated during earlier stages-a pattern also evident in our findings with imidacloprid. Conversely, *Trichogramma pretiosum* (Riley) (Hymenoptera: Trichogrammatidae) pupae were found to be more sensitive to pesticide exposure in terms of developmental period than eggs, larvae, or prepupae (37,38).

Moreover, the longevity of bio-agents, particularly parasitoids, depends upon pesticide type, bioagent species and application techniques (39). A reduction in longevity is commonly observed in parasitoids exposed to insecticides during their development within the host (40). In the present study, exposure to LC_5 and LC_{30} concentrations of imidacloprid led to a significant reduction in female longevity in the F_5 generation, while male longevity was notably reduced at the LC_{50} concentration. Similar findings were reported in a previous study, which documented decreased longevity in *H. hebetor* adults following imidacloprid exposure (41). However, this contrasts with an earlier study where adult longevity remained unaffected by imidacloprid exposure (42). Likewise, divergent outcomes were observed in previous study, where *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) exhibited increased longevity when subjected to LC_5 concentrations of imidacloprid (43). Numerous additional investigations have documented the impact of insecticides on the longevity of *H. hebetor* (13, 29, 44). One study reported adverse effects on *H. hebetor* longevity at LC_{25} concentrations of chlorpyriphos and fenpropathrine (44). However, a previous study reported an improved longevity of the parasitoid with the LC_{25} concentration of profenofos (13).

Furthermore, our study observed a drastic reduction in fecundity in individuals treated with LC_5, LC_{30} and LC_{50} concentrations of imidacloprid. Corroborating these findings, prior research also documented a detrimental impact on the fecundity of *H. hebetor* due to the application of imidacloprid (45). Moreover, adverse effects of imidacloprid, indoxacarb and deltamethrin were also observed on the fecundity of *H. hebetor* (29). However, a reduction in female fecundity with sublethal concentrations of deltamethrin, while no significant observations were noted for sublethal concentrations of imidacloprid and indoxacarb (42). Conversely, an increased fecundity in another parasitoid, *T. chilonis* was observed when exposed to the LC_{30} concentration of imidacloprid (43). These different outcomes are due to the variability in the effects of insecticides on different organisms.

Our investigations revealed a declining trend in oviposition days for individuals subjected to LC_5, LC_{30} and LC_{50} concentrations. In contrast, an extended oviposition period was observed for *H. hebetor* upon exposure to chlorantraniliprole and cyantraniliprole (45). Additionally, there was no influence on the oviposition period of *Bracon nigricans* Szépligeti (Hymenoptera: Braconidae) following exposure to cyantraniliprole (46).

The LC_5 concentration of imidacloprid on *H. hebetor* resulted in a lower R_0, *GRR* and *T* without notable differences in the *r* and λ. In contrast, the LC_{30} concentration demonstrated significant differences in *r* and λ as well as in R_0, *GRR* and *T*. Similarly, exposure to imidacloprid, indoxacarb and deltamethrin significantly lowered the intrinsic rate of increase, finite rate of increase and net reproductive rate of *H. hebetor* (29). It is noteworthy that, across all treatments, R_0 was lower than *GRR*, indicating a substantial impact on survivorship (l_x) attributable to insecticide exposure. The intrinsic rate of increase emerges as a crucial parameter for assessing population development, given its incorporation of age, l_x and the effects of m_x in its calculation (47).

Imidacloprid also had a significant impact on the locomotor activity of *H. hebetor*, resulting in a noteworthy reduction in all the concentrations when compared to the control group. Similar effects were observed in a previous study, where treated *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) exhibited reduced linear speed after exposure to LD_{25} concentrations of deltamethrin, with effects lasting up to 24 h (48).

In another investigation, *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) males showed higher susceptibility (LT_{50} = 24 h) to spinosad than females (LT_{50} = 120 h), indicating sex-specific differences in locomotory responses to insecticide exposure (49). Additionally, *Copidosoma truncatellum* (Dalman) (Hymenoptera: Encyrtidae) displayed a significant increase in walking activity when treated with acephate, methomyl, flubendiamide and indoxacarb (50). Conversely, no significant differences in walking behavior were observed between control and treated groups exposed to chlorantraniliprole, deltamethrin, spinosad and chlorfenapyr.

Considerable research has been dedicated to developing nicotinyl insecticides with high affinity for insect nicotinic acetylcholine receptors (nAChRs), leading to the advent of a novel class of insecticides (51, 52). Neonicotinoids specifically target nAChRs in both the central and peripheral nervous systems, causing neural excitation, followed by paralysis and ultimately leading to insect death (53).

Conclusion

The findings of this study revealed that imidacloprid exerted varying effects on the ectoparasitoid *H. hebetor,* including increased adult longevity in both male and female, along with a reduced pre-adult developmental period, female fecundity and pre-oviposition period across different generations (F_1 and F_5). Notably, this insecticide treatment exhibited deleterious impacts on both biological and population-level parameters. Consequently, a judicious evaluation of their inclusion in IPM programs is crucial. After conducting extensive laboratory studies, it is imperative to shift focus towards semi-field and field experiments to gain practical insights relevant to real-world conditions.

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Authors' contributions

All authors contributed to the study's conception and design. Conceptualization, Methodology, Writing- Original draft preparation: [Basana Gowda G, Prabhu Prasanna Pradhan],

Visualization, Investigation, Validation: [Prabhu Prasanna Pradhan, Umashankar Nayak], Resources: [Totan Adak], Data curation and Analysis: [Guru Prasanna Pandi G], Writing-Reviewing and Editing: [Basana Gowda G, Naveenkumar Basavanagouda Patil, Aishwarya Ray], Supervision, Project administration: [Shyamaranjan Das Mohapatra]. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: There is no visible conflict of interest related to the publication of this article.

Ethical issues: None

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