ORIGINAL CONTRIBUTION

Sublethal effect of beta-cypermethrin on development and fertility of the Asian multicoloured ladybird beetle *Harmonia axyridis*

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Keywords

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Introduction

The Asian multicoloured ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), has been used successfully to control insect pests of crops since the early twentieth century (Colunga-Garcia and Gage 1998). This natural predator has been a component of integrated pest management (IPM) in China but has also become an aggressive invasive

Abstract

The Asian multicoloured ladybird beetle, Harmonia axyridis, is utilized as a major natural enemy of aphids in the field, greenhouses and orchards. However, it has been looked as invasive predator distributing in worldwide. To refine integrated pest management (IPM) against aphids, it is important to evaluate the effects of insecticides on physiology and behaviour of the high adapted predators. Beta-cypermethrin, a broad-spectrum insecticide, not only kills aphids at lethal concentrations but also affects natural enemy of aphids. In our study, the age-stage, two-sex life table was used to evaluating sublethal effects of beta-cypermethrin on the predatory ladybird beetle H. axyridis. In the parent generation, the preoviposition period of *H. axyridis* was significantly shortened (8.93 days) after exposure to LC₅ beta-cypermethrin (5% lethal concentration) as compared with control (10.06 days). However, the oviposition period was significantly longer (46.17 days instead of 43.90 days), and fecundity (eggs per female) was significantly increased by 49.64% when compared with control. In the F_1 generation, the length of the juvenile stage was not affected, but the oviposition period increased significantly (38.19 days compared to 31.39 days in the control). This positive effect was translated to the fecundity that increased significantly by 62.27% as compared with control. According to the life-table analysis, the intrinsic rate of increase (r_m) was significantly higher in treatment (0.140 per day) than that in the control (0.123 per day). In addition, the net reproductive rate (R_0) increased significantly by 91.53%. These results would be useful in assessing the overall effects of beta-cypermethrin on H. axyridis and even for discussing the ecological mechanism of the unexpected extension of H. axyridis during IPM programme.

species in regions where it was introduced (Koch 2003).

Both larvae and adults of *H. axyridis* prey on aphids found on a variety of plants, especially in orchards. However, aphids are controlled mainly through broad-spectrum chemical insecticides in most cropping systems in China. These broad-spectrum insecticides are harmful to beneficial arthropods as well (Desneux et al. 2007). When using IPM to control aphids, their natural enemies may be exposed to pesticides either directly contact with pesticide residues on foliage while foraging on plants or prey (Jepson 1989), or indirectly ingesting pesticide-contaminated food (e.g. prey) (Ahmad et al. 2003; Hua et al. 2004; Torres and Ruberson 2004). The success of IPM programmes depends on the optimal use of selective insecticides that are less harmful to natural enemies (Tillman and Mulrooney 2000; Stark et al. 2007). Such use requires knowledge of the side effects of the selective insecticides on biological and behavioural traits of natural enemies (Liu and Stansly 2004; He et al. 2012; Yu et al. 2014).

From environmental and agronomical points of view, it is important to study the lethal and sublethal effects of insecticides on non-target arthropods. Sublethal effects are defined as physiological and behavioural effects on individuals that survive exposure to a toxic compound at sublethal concentrations or doses (Desneux et al. 2007). The negative impacts of insecticides on non-target organisms have been extensively investigated. In addition to death and reduced fecundity, exposure to a toxicant may result in multiple sublethal effects such as shortened lifespan and oviposition period and changes in oviposition behaviour and fertility rates (Stark and Banks 2003; Stark et al. 2007). Such modifications have undoubtedly important consequences for entire the population of which the exposed individuals are members (Stark and Banks 2003; Stark et al. 2004; Ali et al. 2012; Biondi et al. 2013). Therefore, a demographic analysis of the effects of insecticides, which estimates the total effect of insecticides on whole populations, is crucial to choosing new insecticides as components of IPM programmes. Moreover, the advantages of introduced natural enemies in environment fitness, even positive performance under toxic impacts, could benefit the predators in population colonization and expansion in exotic agroecosystem. Such sublethal insecticides could be looked as a kind of negative-environmental stimulation. In the IPM programme, widely spraving the insecticides with may probably accelerate the invasive processes by promoting their biological performance. Similarly, we also need more empirical evidences to indicate the sublethal effects of these optimized insecticides may impulse the invasive potency of the predators, such as H. axyridis.

Pyrethroids, a group of insecticides derived from natural plant compounds (pyrethrins) isolated from the genus *Chrysanthemum* (Casida 1980), have been used in agricultural and home formulations for over 40 years and account for about 25% of the world market for insecticides. Beta-cypermethrin, which belongs to type II pyrethroids, is a broad-spectrum insecticide used worldwide for controlling insect pests in row crops, fruits and vegetables. Various lethal and sublethal effects of beta-cypermethrin on various insect pests have been reported recently (Han et al. 2011; Song et al. 2013; Wang et al. 2014). However, its potential sublethal effects and the consequent demographic changes on natural enemies have not been adequately documented so far. The objective of this study was to explore the sublethal effects of betacypermethrin on development, fertility and demographic parameters of *H. axyridis* under laboratory conditions. The results would provide useful insights into the overall effects of beta-cypermethrin on H. axyridis and benefit in optimizing its use as a component of an effective pest management strategy in the field.

Materials and Methods

Insect rearing

Adults of *H. axyridis* were collected from experimental cotton fields (39°95'N, 116°28'E) of the Beijing Academy of Agriculture and Forestry Sciences (BAAFS), Beijing, China, in May 2013. The beetles were reared in the Laboratory of Natural Enemies Research, Institute of Plant and Environment Protection, BAAFS, on the aphid Aphis craccivora Koch (Hemiptera: Aphididae) to establish the experimental population. The population was maintained in cages $(50 \times 50 \times$ 60 cm) made of aluminium frames covered with 100mesh plastic gauze). Each cage housed 40 pairs of adults that were fed daily with aphids which were reared on fresh seedlings of broad bean (Vicia faba L. 'LinCan-5') (Wang et al. 2013). The ambient environment was regulated using an automatic environmental management system (Sunauto, Beijing, China) at $25 \pm 1^{\circ}$ C and 70% relative humidity, with 16 h of light (1200 lux) alternating with 8 h of darkness.

Insecticide and acute toxicity assessment

Technical grade beta-cypermethrin (95%) was bought from Jiangsu Changlong Chemical Co., Ltd (Jiangsu, China). The toxicity of beta-cypermethrin to *H. axyridis* was assessed by minor modifications to the method described by He et al. (2012), which involves exposing the insects to pesticide residues in glass tubes. Based on preliminary experiments to establish the range of concentrations to be tested, six concentrations of beta-cypermethrin were used for the bioassay, starting with 5 mg/l and doubling the concentration successively to reach 160 mg/l. An aliquot of 820 μ l of the insecticide solution in acetone was placed in each glass tube (14.5 cm long with a diameter of 1.5 cm). These tubes were immediately rotated using a micro-rotator (American Wheaton Company) until their insides had been evenly coated with the insecticide residue. Twenty adults of *H. axyridis* (5 days old) were exposed to each concentration with three replications. Controls were maintained using acetone alone. The ladybird beetles were reared for 24 h under the laboratory conditions described above. Mortality was recorded after the exposure and individuals that failed to react when pushed with a brush were considered dead (He et al. 2012).

 LC_5 was chosen as the sublethal concentration of beta-cypermethrin and its acute toxicity to 5-day-old adults of *H. axyridis* was assessed using the methodology described above, using nine replicates, each with 20 adults maintained for 24 h under the same ambient conditions mentioned above. Mortality was assessed 24 h after the exposure as described above.

Sublethal effects on *H. axyridis* in the parent generation

The LC₅ of beta-cypermethrin for *H. axyridis* was 3.158 mg/l as calculated based on the regression equation (see result section). The effects of exposure to a sublethal concentration (LC₅) of beta-cypermethrin on the development and fecundity of *H. axyridis* were assessed. The insects were exposed to the insecticide as described above. Adult females and males were paired and transferred to new plastic cups (7 cm in diameter and 9 cm deep) covered with a fine nylon net (45) mesh for ventilation and provided daily with fresh bean leaves infested with 50–100 aphids. If the male predeceased the female, another adult male was introduced into the cup. Three replicates were maintained, each with 20 pairs.

Life table of *H. axyridis* in F₁ generation

To estimate the impact of beta-cypermethrin on development and fecundity in F_1 generation of *H. axyridis,* the numbers of surviving juveniles and adults were recorded daily to generate the demographic parameters. Eggs from the parent generation (exposed to beta-cypermethrin) were collected within 24 h after they had been laid and transferred to new petri dishes (9 cm in diameter) for life-table studies. Each first-instar larva was moved to a fresh plastic cup, kept in a growth chamber under the conditions mentioned above and fed daily with a

fresh leaf infested with 50–100 aphids. Data on survival and development were recorded daily until pupation. Newly emerged adults were paired, then moved to new plastic cups and fed daily with adequate numbers of aphids. Data on fecundity (the number of eggs produced) and lifespan were recorded daily until death. If the male predeceased the female, another adult male was introduced into the cup as a substitute. Data for the substitute were not included in the data analysis.

Life-table analysis

The development time, survivorship, longevity of individuals and female daily fecundity of H. axyridis were analysed according to the age-stage, two-sex life-table theory (Chi and Liu 1985; Chi 1988) using a computer program TWOSEX-MSChart (Laboratory of Theoretical and Applied Ecology, Department of Entomology, National Chung Hsing University, Taiwan; Chi 2013). The age-stage-specific survival rate S_{xi} (x = age, j = stage) is the probability that an individual, after emerging from a newly laid egg, will survive to age x and stage j; the reproductive value (V_{xi}) is defined as the contribution of an individual of age *x* and stage *j* to the future population; the life expectancy (e_{xi}) is the period that an individual of age x and stage j is expected to live; the age-specific survival rate (l_x) is the age-specific survival rate (the proportion of individuals from the initial cohort alive at a given age); f_x is the female age-specific fecundity, and m_x is age-specific fecundity of the total population.

The demographic parameters were (i) net reproductive rate $(R_0 = \sum l_x m_x)$: the population growth rate per generation with regard to the number of female offspring produced per female, l_x is the proportion of individuals surviving to age *x*, and m_x is the number of female produced per female of age x; (ii) mean generation time $(T = \sum x l_x m_x / R_0)$: the average interval separating births from one generation to the next; (iii) intrinsic rate of natural increase $(r_m = \ln(R_0)/T)$: the maximum exponential increase rate in a population growing within defined physical condition, the r_m was calculated using the iterative bisection method and the Euler-Lotka equation with the age indexed from 0: $\sum l_x m_x \exp(-r_m x) = 1$; and (iv) finite rate of increase $(\lambda = \exp(r_m))$: the factor by which a population multiplies. These four demographic parameters were obtained from the computer program, which includes a routine for estimating the standard error of demographic parameters using the bootstrap technique.

Statistical analysis

The LC₅₀ value was determined using a log-probit model (Finney 1971). The dose–mortality relationships were considered valid (i.e., they fitted the observed data) when the observed data and the expected data did not diverge significantly (P < 0.05). PoLoPlus ver. 2.0 (LeOra Software, Petaluma, CA, USA) was used for the analysis. The mortality of adults exposed to beta-cypermethrin was analysed by *t*-test using ProStat (Poly Software International, Pearl River, NY, USA).

The TWOSEX-MSChart computer program was used to calculate the demographic parameters (Chi 2013), and the bootstrap technique (Efron and Tibshirani 1993) was used to calculate their mean and standard error. Because bootstrapping uses random resampling, a small number of replications will generate variable means and standard errors. To reduce the variability, we used 10 000 replications in this study. Differences in life-history traits of *H. axyridis* between the control and the treatment group were compared using *t*-tests at 5% level of significance using ProStat software (Poly Software International, Pearl River, NY, USA). Difference in demographic parameters between the control and the treatment group was compared using *t*-test by the TWOSEX-MSChart computer program.

Results

Concentration-mortality response and acute toxicity

Based on the log-probit regression analyses, the LC₅₀ of beta-cypermethrin for H. axyridis was estimated at 26.17 mg/l (95% confidence interval: 20.63-30.59 mg/l; regression equation: Y = 1.821X + 2.446, $\chi^2 = 0.50$, P = 0.233). The data fitted the linear model (no statistically significant deviation of data from the regression equation). The LC5 of beta-cypermethrin for H. axyridis was 3.158 mg/l as calculated based on the regression equation. The LC5 of beta-cypermethrin led to $5.56 \pm 1.94\%$ mortality (corrected mortality; Abbott 1925). This concentration induced no significant mortality when compared to the control (P < 0.05, *t*-test: t = 0.936; P = 0.377). Thus, the LC₅ of beta-cypermethrin was classified as sublethal concentration according to Desneux et al. (2007), namely those that induce no statistically significant mortality in the experimental population.

Sublethal effects on longevity and fecundity in parent generation

The effects of LC₅ beta-cypermethrin on longevity and fecundity of *H. axyridis* in the parent generation

are shown in fig. 1. The pre-oviposition period decreased significantly (8.93 \pm 0.15 days) compared to that in the control group (10.06 \pm 0.21 days) (fig. 1a; t = 4.335, P < 0.001), whereas the oviposition period increased significantly (46.17 \pm 0.58 days in treatment; 43.90 \pm 0.67 days in control) (fig. 1b; t = 2.836, P < 0.001). There is no significant difference of adult longevity between the control and the treatment group (fig. 1c; t = 1.438, P = 1.161). The fecundity (eggs per female) increased significantly (1008.60 \pm 15.53) as compared with control (674.03 \pm 17.37) (fig. 1d; t = 16.49, P < 0.001).

Sublethal effects on development, longevity and fecundity in F_1 generation

The sublethal effects of beta-cypermethrin on the duration of each developmental stage, adult longevity, preoviposition period, oviposition period and fecundity in F_1 generation are given in table 1. There were no significant differences with respect to the time taken by the egg to hatch and the duration of each instar between the control and the treatment group. However, the pupal stages were significantly shorter in treatment group when compared with control (t = 2.382, P = 0.019). In addition, the pre-adult (duration of egg to adult emergence) was also significantly shorter in treatment group as compared with control (t = 2.332, P = 0.022). There was no significant difference of adult longevity between control and treatment group (t = 1.603, P = 0.113). The longevity of females in the treatment group was significantly longer when compared with control (t = 2.038, P = 0.047). However, no effect on longevity of males when the parent generation exposed to beta-cypermethrin (t = 0.127, P = 0.899).

The adult pre-oviposition period (APOP) refers to the beginning of adult stage, and the total pre-oviposition period (TPOP) is counted from the beginning of the life-table study to production of the first egg. Both periods were significantly shorter in the treatment group when compared with their respective control (t = 2.691, P = 0.009; t = 2.765, P = 0.008). The oviposition period was significantly longer by 17.80% as compared with control (t = 5.691, P < 0.001). This positive effect was reflected in the significantly increased fecundity (eggs per female), an increase of 62.44% over that in the control group. (t = 11.14, P < 0.001) (table 1).

Sublethal effects on survival rate, fecundity, life expectancy and reproduction value in F₁ generation

The age-stage-specific survival rate (S_{xj}) represents the probability that an egg will produce an individual

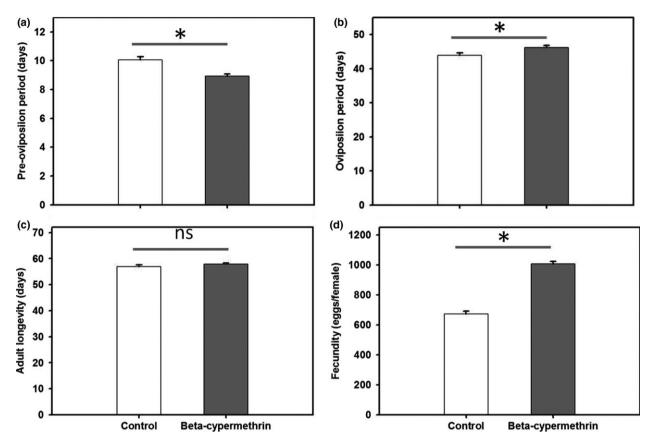


Fig. 1 Effects of sublethal concentration of beta-cypermethrin on pre-oviposition period (a), oviposition period (b), adult longevity (c) and fecundity (d) of *Harmonia axyridis* in parent generation. The results are means (\pm SEM), and the asterisk indicates significant differences based on the *t*-test (P < 0.05).

Table 1 Sublethal effects of	f beta-cypermethrin or	n developmental time	and fecundity or	n Harmonia axvridis in E	generation
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	Control		Beta-cypermethrin		Statistic		
Developmental time (days)		$\text{Mean} \pm \text{SE}$	n	$\text{Mean} \pm \text{SE}$	Ρ	t	d.f.
Egg	60	3.10 ± 0.046	60	3.10 ± 0.039	0.999	0.000	118
First instar	52	2.71 ± 0.063	53	2.58 ± 0.068	0.178	1.357	103
Second instar	47	2.89 ± 0.055	49	2.90 ± 0.053	0.954	0.057	94
Third instar	44	3.00 ± 0.056	49	3.02 ± 0.054	0.795	0.260	91
Fourth instar	44	4.00 ± 0.065	47	4.02 ± 0.048	0.791	0.266	89
Рира	44	6.48 ± 0.10	47	$6.17\pm0.082\textbf{*}$	0.019	2.382	89
Pre-adult	44	22.09 ± 0.112	47	$21.74\pm0.098\textbf{*}$	0.022	2.332	89
Adult longevity	44	51.68 ± 1.085	47	53.85 ± 0.826	0.113	1.603	89
Total longevity	44	56.18 ± 3.878	47	60.93 ± 3.693	0.175	1.369	89
Female	23	74.48 ± 1.44	27	$77.30\pm0.36\textbf{*}$	0.047	2.038	48
Male	21	73.00 ± 1.58	20	73.30 ± 1.77	0.899	0.127	39
Adult pre-oviposition period of female adult (APOP)	21	9.65 ± 0.31	20	$8.74\pm0.17\textbf{*}$	0.009	2.691	48
Total pre-oviposition period of female counted from birth (TPOP)	21	31.83 ± 0.348	20	$30.63\pm0.268\textbf{*}$	0.008	2.765	48
Oviposition period	21	31.39 ± 1.16	20	$38.19\pm0.49\textbf{*}$	< 0.001	5.691	48
Fecundity (offspring)	23	649.26 ± 33.17	27	1053.56 ± 18.07*	< 0.001	11.14	48

*Significant differences in the same row based on *t*-test using ProStat software (P < 0.05).

who survives to age *x* and stage *j*. The significantly positive effects of beta-cypermethrin on the age-stage survival rate in adults are evident in fig. 2. The life expectancy (e_{xi}) of *H. axyridis* – the duration for which an individual who has attained age x and stage *i* is expected to live after attaining that age – is plotted in fig. 3: the two groups did not differ significantly in terms of that parameter. The reproductive value (V_{xi}) is the contribution of individual of age *x* and stage *j* to the future population: females near the peak of their reproductive ability contribute considerably more to the population than those at other ages and stages. Exposure to LC₅ beta-cypermethrin increased the reproductive value. In control, a 35-day-old female had a markedly higher reproductive value, 164.06, whereas a 35-day-old female exposed to LC5 betacypermethrin had the highest reproductive value of 203.6 (fig. 4). The age-specific survival rate (l_x) , female age-specific fecundity (f_x) and age-specific fecundity of the total population (m_x) are shown in

fig. 5. The curve of l_x is a simplified version of S_{xj} . The survival rate and fecundity of the exposed population were greater than those of the respective control groups: the maximum value of f_x in the control group was 24.96 eggs at 37 day, compared to 35.15 at 51 day in the treatment group.

Sublethal effects on demographic parameters in F₁ generation

The means and standard errors of the demographic parameters as calculated using the bootstrap technique are presented in table 2. The intrinsic rate of increase (r_m) was significantly higher in the treatment population (0.140 per day) as compared to the control (0.123 per day). The similar variation tendency was observed in the finite rate of increase (λ) and the net reproduction rates (R_0). The R_0 obtained in treatment group (474.79 offspring) was significantly higher than control group (247.89 offspring). The mean genera-

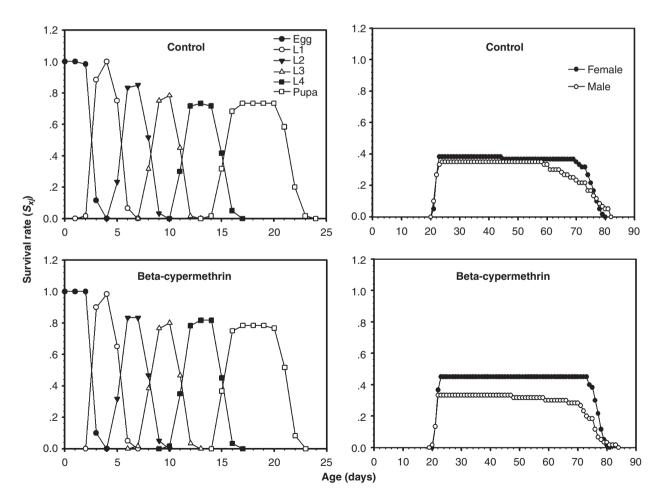


Fig. 2 Effect of sublethal concentration of beta-cypermethrin on the survival rate (S_{xi}) of Harmonia axyridis in F₁ generation.

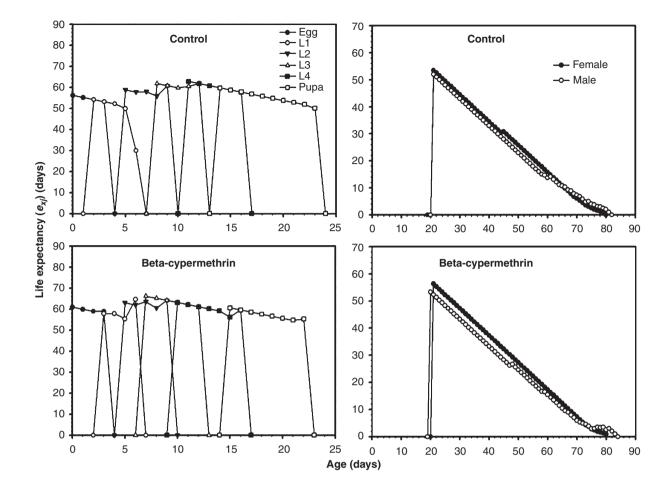


Fig. 3 Effect of sublethal concentration of beta-cypermethrin on the life expectancy (E_{xi}) of Harmonia axyridis in F₁ generation.

tion time (*T*), on the other hand, was significantly lower in the treatment group (43.86 days) when compared with control (44.58 days).

Discussion

The role of natural enemies as biological control agents is well recognized and extensively documented (Symondson et al. 2002). *H. axyridis*, an effective agent in controlling aphids, is likely to be exposed to relatively low concentrations of broad-spectrum beta-cypermethrin because it is widely used in orchards in China. Therefore, apart from the acute lethal effects that usually occur at high doses, the natural enemies may also be exposed to sublethal doses of insecticide. The side effects of pesticides on natural enemies warrant a more ecologically relevant endpoint as a measure of effect (Desneux et al. 2007; Stark et al. 2007). In the present study, we provide experimental evidence of the sublethal and stimulatory effects of

reduced concentrations of beta-cypermethrin on *H. axyridis* that demonstrate a longer oviposition period, higher reproductive levels and enhanced population growth in both the parent and F_1 generation.

The pre-oviposition period of H. axyridis in both the parent and F₁ generations was significantly shortened compared to that in the respective control groups. This result was consistent with an earlier report that the third-instar nymphs of Supputius cincticeps exposed to very low doses of permethrin developed into females with a shorter pre-oviposition period (Zanuncio et al. 2003). However, in the present experiment, the oviposition period in individuals exposed to the insecticide turned out to be significantly longer: H. axyridis showed a compensatory response to interference with its development, as suggested by Townsend and Luckey (1960), in the form of a longer duration of one instar and a shorter duration of another. This response may be explained as hormesis, which is based on the allocation of available energy

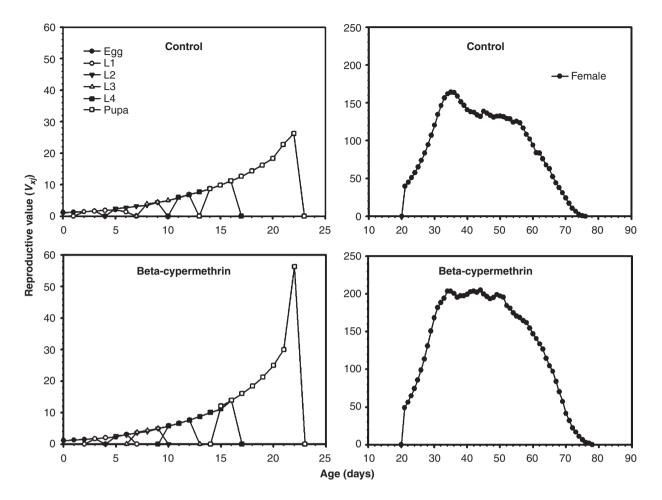


Fig. 4 Effect of sublethal concentration of beta-cypermethrin on the reproduction value (V_{xi}) of Harmonia axyridis in F₁ generation.

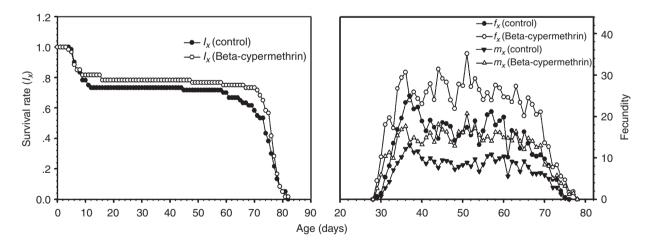


Fig. 5 Effect of sublethal concentration of beta-cypermethrin on survival rate (l_x) , female age-specific fecundity (f_x) and age-specific fecundity (m_x) of *Harmonia axyridis* in F₁ generation.

(Sibly and Calow 1986) to different physiological processes by lowering the value of one parameter and raising the value of another. The side effects of a pesticide include not only the individual mortality and field performance of a given natural enemy but also its population dynamics.

	Estimated by using bootstrap method						
Demographic parameter	Control	Beta-cypermethrin	d.f.	t	Р		
Intrinsic rate of increase: r_m (per day)	0.123 ± 0.005	0.140 ± 0.004*	118	20.97	<0.05		
Finite rate of increase: λ (per day)	1.313 ± 0.005	$1.151 \pm 0.005*$	118	11.04	< 0.05		
Net reproductive rate: R_0 (offspring/individual)	247.89 ± 42.82	474.79 ± 68.32*	118	21.68	< 0.05		
Mean generation time: T	44.58 ± 0.50	$43.86\pm0.414\textbf{*}$	118	7.14	< 0.05		

Table 2 Sublethal effect of beta-cypermethrin on demographic parameters of Harmonia axyridis in F1 generation

*Significant differences in the same row based on t-test using TWOSEX-MSChart computer program (P < 0.05).

Demographic parameters are particularly useful in assessing sublethal effects at the population level and are also essential in estimating population growth in ecological studies (Stark and Banks 2003; Biondi et al. 2013). Life tables are one of the most useful tools in the study of insect population dynamics (Gao and Yang 2015). The age-stage, two-sex life table includes both sexes as well as variable development rates among individuals and has been used in studying many members of Coccinellidae; for example, population dynamics of Cheilomenes sexmaculata under different conditions (Zhao et al. 2015) and predation rates of Lemnia biplagiata (Yu et al. 2005), Hippodamia variegate (Farhadi et al. 2011), and Harmonia dimidiate (Yu et al. 2013). In addition, the life table was used to evaluate the effect of the herbicide glyphosate on the predatory insect Chrysoperla externa (Schneider et al. 2009).

The age-stage, two-sex life table was used to evaluate the effect of sublethal concentration of beta-cypermethrin on *H. axyridis*. Under laboratory conditions, the mean values of the intrinsic increase rate (r_m) and the net reproductive rate (R_0) tended to be higher in the treatment groups than in the corresponding control groups (table 2). All these traits affect population fitness profoundly. The demographic approach followed in the present study demonstrates that betacypermethrin at a low concentration (LC₅) stimulated fecundity (eggs per female).

Hormesis refers to possible enhanced performance of individuals at low levels of exposure to toxic agents that are harmful at high levels of exposure (Calabrese and Baldwin 2003). The phenomenon has been reported in many arthropod pests and natural enemies, and it has been linked to pest outbreaks and potential problems due to insecticide resistance (Guedes and Cutler 2014). In the present study, we ascertained whether hormesis, especially with reference to fecundity traits, occurs in *H. axyridis* during or after exposure to a sublethal concentration of betacypermethrin: our findings indicate that it does, as

shown by a 49.64% increase in fecundity in the parent generation. Moreover, the enhanced reproduction was also showed in the F_1 generation as well (the increase was 62.27%). These results can be ascribed to hormesis as defined by Calabrese and Baldwin (2001). The stimulated reproduction observed in the present study is consistent with that a sublethal concentration of beta-cypermethrin stimulated population growth in Plutella xylostella (Han et al. 2011). Similar results were reported for other pyrethroid insecticides: for instance, P. xylostella laid more eggs after being exposed to sublethal doses of fenvalerate (Sota et al. 1998; Fujiwara et al. 2002) and application of synthetic pyrethroids led to a resurgence of A. gossypii in cotton (Nandihalli et al. 1992). More recently, outbreaks of red mite were attributed to deltamethrin-induced hormesis (Cordeiro et al. 2013). Hormesis has also been reported with other insecticides; for example, laboratory experiments suggest that exposure to sublethal concentrations of imidacloprid could stimulate reproduction in Myzus persicae (Cutler et al. 2009; Yu et al. 2010) and in A. glycines (Qu et al. 2015).

The success of IPM programme depends on the optimal use of selective insecticides that are less harmful to natural enemies of pests (Tillman and Mulrooney 2000; Stark et al. 2007). And the coordination with pesticides directly affects the control effect of natural enemies. As the benefits to the natural enemy, the sublethal effects of the pesticides may impulse the population colonization and expansion of the predators, as our results showed that sublethal concentration of beta-cypermethrin affected H. axyridis favourably by stimulating its fecundity: this observation indicates the potential of combining the application of beta-cypermethrin with the release predatory species at a suitable time as a component of IPM programme. Due to the high adaptability of invasive natural enemy insects, they can successfully colonize to adverse environment and replace other predator. H. axyridis was considered as aggressive

invasive species in the introduced regions. In our study, the fitness of *H. axyrids* was increased because sublethal concentration of beta-cypermethrin induced the higher reproduction. The positive reaction to insecticide stress may contribute the high invasive ability of *H. axyridis*. In addition, further studies on the mechanism of hormesis induced by beta-cypermethrin in *H. axyridis* would be certainly worthwhile.

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Conflict of Interest

The authors have declared that no competing interests exist.

References

- Abbott WS, 1925. A method for computing the effectiveness of an insecticide. J Econ Entomol 18, 265–267.
- Ahmad M, Ossiewatsch HR, Basedow T, 2003. Effects of neem-treated aphids as food/hosts on their predators and parasitoids. J Appl Entomol 127, 458–464.
- Ali A, Ahmad F, Biondi A, Wang Y, Desneux N, 2012. Potential for using Datura alba leaf extracts against two major stored grain pests, the khapra beetle *Trogoderma granarium* and the rice weevil *Sitophillus oryzae*. J Pest Sci 85, 359–366.
- Biondi A, Zappalà L, Stark JD, Desneux N, 2013. Do biopesticides affect the demographic traits of a parasitoid wasp and its biocontrol services through sublethal effects? PLoS ONE 8, e76548.
- Calabrese EJ, Baldwin LA, 2001. Hormesis: a generalization and unifying hypothesis. Crit Rev Toxicol 31, 353– 424.
- Calabrese EJ, Baldwin LA, 2003. Toxicology rethinks its central belief-Hormesis demands a reappraisal of the way risks are assessed. Nature 421, 691–692.
- Casida JE, 1980. Pyrethrum flowers and pyrethroid insecticides. Environ Health Perspect 34, 189–202.
- Chi H, 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. Environ Entomol 17, 26–31.

- Chi H, 2013. TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. http:// 140.120.197.173/Ecology/. National Chung Hsing University, Taichung, Taiwan.
- Chi H, Liu H, 1985. Two new methods for the study of insect population ecology. Bull Inst Zool 24, 225–240.
- Colunga-Garcia M, Gage SH, 1998. Arrival, establishment, and habit use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environ Entomol 27, 1574–1580.
- Cordeiro EMG, de Moura ILT, Fadini MAM, Guedes RNC, 2013. Beyond selectivity: are behavioral avoidance and hormesis likely causes of pyrethroid-induced outbreaks of the southern red mite *Oligonychus ilicis*? Chemosphere 93, 1111–1116.
- Cutler GC, Ramanaidu K, Astatkiec T, Ismana MB, 2009. Green peach aphid, *Myzus persicae* (Hemiptera: Aphididae), reproduction during exposure to sublethal concentrations of imidacloprid and azadirachtin. Pest Manag Sci 65, 205–209.
- Desneux N, Decourtye A, Delpuech JM, 2007. The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 52, 81–106.
- Efron B, Tibshirani RJ, 1993. An introduction to the bootstrap. Chapman and Hall, New York, NY.
- Farhadi R, Allahyari H, Chi H, 2011. Life table and predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae) feeding on *Aphis fabae* (Hemiptera: Aphididae). Biol Control 59, 83–89.
- Finney DJ, 1971. Probit analysis. Cambridge University Press, Cambridge.
- Fujiwara Y, Takahashi T, Yoshioka T, Nakasuji F, 2002. Changes in egg size of the diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) treated with fenvalerate at sublethal doses and viability of the eggs. Appl Entomol Zool 37, 103–109.
- Gao SK, Yang ZQ, 2015. Application of life table in pest biological control. Chin J Biol Control 31, 256–263.
- Guedes RNC, Cutler GC, 2014. Insecticide-induced hormesis and arthropod pest management. Pest Manag Sci 70, 690–697.
- Han WS, Zhang SF, Shen FY, Zhang HJ, Gao XW, 2011. Sublethal effects of beta-cypermethrin on abamectinresistant and –susceptible population of diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae). J Environ Entomol 33, 335–341.
- He YX, Zhao J, Zheng Y, Zhan Z, Desneux N, Wu KM, 2012. Lethal effect of imidacloprid on the coccinellid predator *Serangium japonicum* and sublethal effects on predator voracity and on functional response to the whitefly *Bemisia tabaci*. Ecotoxicology 21, 1291–1300.
- Hua RM, Cao HQ, Xu GW, Tang F, Li XD, 2004. The integrative toxicity effects of beta-cypermethrin on *Propylea japonica* larvae and *Aphis gossiypii* adults. Acta Phytophylacica Sinica 31, 96–100.

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Koch RL, 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. J Insect Sci 3, 32.

Liu TX, Stansly PA, 2004. Lethal and sublethal effects of two insect growth regulators on adult *Delpgatus catalinae* (Coleoptera: Coccinellidae), a predator of whiteflies (Homoptera: Aleyrodidae). Biol Control 30, 298–305.

Nandihalli BS, Patil BV, Hugar P, 1992. Influence of synthetic pyrethroid usage on aphid resurgence in cotton, Karnataka. J Agr Sci 5, 234–237.

Qu YY, Xiao D, Li JY, Chen Z, Biondi A, Desneux N, Gao XW, Song DL, 2015. Sublethal and hormesis effects of imidacloprid on the soybean aphid *Aphis glycines*. Ecotoxicology 24, 479–487.

Schneider MI, Sanchez N, Pineda S, Chi H, Ronco A, 2009. Impact of glyphosate on the development, fertility and demography of Chrysoperla externa (Neuroptera: Chrysopidae): ecological approach. Chemosphere 76, 1451–1455.

Sibly RM, Calow P, 1986. Physiological ecology of animals —an evolutionary approach. Blackwell, Scientific Publications, Oxford.

Song L, Zhang JM, Lv YB, 2013. Sublethal effects of indoxacarb and beta-cypermethrin on *Plutella xylostella* (Lepidoptera: Plutellidae). Acta Entomologica Sinica 56, 521–529.

Sota N, Motoyama N, Fujisaki K, Nakasuji F, 1998. Possible amplification of insecticide hormoligosis from resistance in the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae). Appl Entomol Zool 33, 435–440.

Stark JD, Banks JE, 2003. Population-level effects of pesticides and other toxicants on arthropods. Annu Rev Entomol 48, 505–519.

Stark JD, Banks JE, Vargas R, 2004. How risky is risk assessment: the role that life history strategies play in susceptibility of species to stress. Proc Natl Acad Sci USA 101, 732–736.

Stark JD, Vargas RI, Banks JE, 2007. Incorporating ecologically relevant measures of pesticide effect for estimating the compatibility of pesticides and biocontrol agents. J Econ Entomol 100, 1027–1032.

Symondson WO, Sunderland KD, Greenstone MH, 2002. Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47, 561–594.

Tillman PG, Mulrooney JE, 2000. Effect of selected insecticides on the natural enemies *Colleomegilla maculata*

and *Hippodamia convergens* (Coleoptera: Coccinellidae), *Geocoris punctipes* (Hemiptera: Lygaeidae), and *Bracon mellitor*, Cardiochiles nigriceps, and Cotesia marginiventris (Hymenoptera: Braconidae) in cotton. J Econ Entomol 93, 1638–1643.

Torres JB, Ruberson JR, 2004. Toxicity of thiamethoxam and imidacloprid to *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) nymphs associated to aphid and whitefly control in cotton. Neotrop Entomol 33, 99–106.

Townsend CO, Luckey TD, 1960. Hormoligosis in pharmacology. J Am Med Assess 173, 44–48.

Wang S, Michaud JP, Tan XL, Murray L, Zhang F, 2013. Melanism in a chinese population of *Harmonia axyridis* (Coleoptera: Coccinellidae): a criterion for male investment with pleiotropic effects on behavior and fertility. J Insect Behav 26, 679–689.

Wang XQ, Liu CZ, Xing YT, Shi Z, 2014. Effects of sublethal dosages of imidacloprid, abamectin and betacypermethrin on the development and reproduction of green of the morph of pea aphid (*Acyrthosiphon pisum*). Acta Prataculturae Sinica 23, 279–286.

Yu JZ, Chi H, Chen BH, 2005. Life table and predation of *Lemnia biplagiata* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) with a proof on relationship among gross reproduction rate, net reproduction rate and preadult survivorship. Ann Entomol Soc Am 98, 475–482.

Yu YS, Shen GQ, Zhu HL, Lu YT, 2010. Imidaclopridinduced hormesis on the fecundity and juvenile hormone levels of the green peach aphid *Myzus persicae* (Sulzer). Pestic Biochem Physiol 98, 238–242.

Yu JZ, Chi H, Chen BH, 2013. Comparison of the life tables and predation rates of *Harmonia dimidiate* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Hemiptera: Aphididae) at different temperatures. Biol Control 64, 1–9.

Yu CH, Lin RH, Fu MR, Zhou YM, Zong FL, Jiang H, Lv N, Piao XY, Zhang J, Liu YQ, Brock TCM, 2014. Impact of imidacloprid on life-cycle development of *Coccinella septempunctata* in laboratory microcosms. Ecotox Environ Safe 110, 168–173.

Zanuncio TV, Serrao JE, Zanuncio JC, Guedes RNC, 2003. Permethrin induced hormesis on the predator Supputius cincticeps (Stal, 1860) (Heteroptera: Pentatomidae). Crop Prot 22, 941–947.

Zhao J, Li S, Gao XW, Zhang F, Wang S, 2015. Comparison of life tables of *Chelomenes sexmaculata* (Coleoptera: Coccinellidae) under laboratory and greenhouse conditions. J Econ Entomol 108, 1700–1707.