





The green lacewing *Chrysopa formosa* as a potential biocontrol agent for managing *Spodoptera frugiperda* and *Spodoptera litura*

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Abstract

Understanding predator–prey interactions is essential for successful pest management by using predators, especially for the suppression of novel invasive pest. The green lacewing *Chrysopa formosa* is a promising polyphagous predator that is widely used in the biocontrol of various pests in China, but information on the control efficiency of this predator against the seriously invasive pest *Spodoptera frugiperda* and native *Spodoptera litura* is limited. Here we evaluated the predation efficiency of *C. formosa* adults on eggs and first- to third-instar larvae of *S. frugiperda* and *S. litura* through functional response experiments and determined the consumption capacity and prey preference of this chrysopid. Adults of *C. formosa* had a high consumption of eggs and earlier instar larvae of both prey species, and displayed a type II functional response on all prey stages. Attack rates of the chrysopid on different prey stages were statistically similar, but the handling time increased notably as the prey developed. The highest predation efficiency and shortest-handling time were observed for *C. formosa* feeding on *Spodoptera* eggs, followed by the first-instar larvae. *C. formosa* exhibited a significant preference for *S. litura* over *S. frugiperda* in a two-prey system. In addition, we summarized the functional response and predation efficiency of several chrysopids against noctuid pests and made a comparison with the results obtained from *C. formosa*. These results indicate that *C. formosa* has potential as an agent for biological control of noctuid pests, particularly for the newly invasive pest *S. frugiperda* in China.

Introduction

The invasive fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and the common cutworm, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae), are both extremely polyphagous and cosmopolitan pests that undergo widespread dispersal and can feed on many economically important crops, such as maize, sorghum, wheat, cotton, groundnut, soybean and vegetables (Rao *et al.*, 1993; Montezano *et al.*, 2018). Their early instar larvae feed gregariously on plant leaves, and later instars are highly voracious and can attack most parts of the plant, often causing severe damage to crops (Sparks, 1979; Gupta *et al.*, 2015). Infestations of *S. frugiperda* can cause yield losses of 15–73% in maize (Hruska and Gould, 1997), and maize crops worth USD 18 billion per year have been at risk of fall armyworm damage throughout Africa, the Near East and the Asia-Pacific region since its invasion (FAO, 2020). The economic loss caused by *S. litura* can reach between 25.8 and 100% in crops (Dhir *et al.*, 1992). Because of their high reproductive capacity and associated heavy crop losses, *S. frugiperda* and *S. litura* are considered to be the most destructive insect pests in many countries of the Asia-Pacific region, including China, Japan, India and Pakistan, where these two species threaten agricultural production, food security and the livelihoods of farmers (Ahmad *et al.*, 2013; Early *et al.*, 2018; FAO, 2020).

Currently, management of *S. frugiperda* and *S. litura* depends mostly on application of various insecticides. However, many field populations of *S. frugiperda* and *S. litura* have developed high resistance to conventional and newer insecticides, which leads to frequent failures with chemical pest control (Ahmad *et al.*, 2008; Tong *et al.*, 2013; Gutierrez-Moreno *et al.*, 2019; Wan *et al.*, 2021). An alternative and ecologically friendly control strategy against *S. frugiperda* and *S. litura* is biological control using natural enemies. As a key component of integrated pest management, biological control has been successfully applied against a wide range of agricultural pests throughout the world during the past 130 years (Bale *et al.*, 2008). Many studies have also shown that biological control is the most environmentally safe and economically profitable pest management method (Bale *et al.*, 2008; Van Lenteren, 2011; Yang *et al.*, 2014).

Green lacewings are proven broad-spectrum biological control agents against a variety of soft-bodied pests, including aphids, whiteflies, thrips, mites and scales, as well as eggs and small larvae of Lepidoptera and Coleoptera (Canard *et al.*, 1984; McEwen *et al.*, 2010). The efficiency of several

chrysopid species in the family of Chrysopidae, such as *Chrysopa pallens* (Rambur), *Chrysoperla sinica* (Tjeder) and *Chrysoperla carnea* (Stephens), in controlling *S. frugiperda* and *S. litura* has been well recognized (Tauber et al., 2000; McEwen et al., 2010; Huang et al., 2020; Li et al., 2020). However, there is a limited number of chrysopid species that can be used commercially for release in biological control programs, and there is an urgent need to exploit other species and to evaluate their predation efficiency. The polyphagous predator *Chrysopa formosa* (Brauer) is widely distributed in the region of Asia and Europe, and it is a very efficient predator of many kinds of pests, as both its larvae and adult feed on prey (Li et al., 2018). This predator has been successfully mass-reared within insectaries and released into cotton fields and greenhouses for controlling several pests, including aphids, whiteflies, spider mites and cotton bollworm, in China (Yang et al., 2014; Zhou et al., 2014; Lai and Liu, 2020). *C. formosa* may be a good candidate for suppressing the invasive pests *Hyphantria cunea* (Drury) (Nan et al., 2019), *Aleurodicus dispersus* (Russell) (Li et al., 2010) and *Dysmicoccus neobrevipes* (Beardsley) (Yan, 2012). In our previous studies, we showed that the second- and third-instar larvae of *C. formosa* have a high predation on eggs and young larvae of *S. frugiperda* and *S. litura* (Li et al., 2021; Wang et al., 2022). In contrast, the ability of the chrysopid adult to prey on these two *Spodoptera* pests has not been studied. Thus, the aim of this study was to evaluate the predation efficiency of *C. formosa* adults toward *S. frugiperda* and *S. litura*.

The functional response of a predator refers to the number of prey consumed at different prey densities, and it defines the capacity of a predator to adjust its predation rate to the changing density of its prey (Solomon, 1949). The functional response is commonly used to assess the efficiency of predators in regulating the population of their prey, because it is an important component in the predator-prey dynamics (Hassanpour et al., 2011; Van Lenteren et al., 2016; Feng et al., 2018). Three types of functional responses in relation to prey density have been described by Holling (1959). Type I is represented by a linear increase in the predation rate, type II corresponds to an increase at a decelerating rate to a plateau and type III is represented as a sigmoid increase. The analysis of functional response characteristics is important for understanding predation efficiency of a predator and for evaluating the potential of a predator as a candidate for biological control programs (Cuthbert et al., 2018; Pan et al., 2019; Qin et al., 2019; Viteri Jumbo et al., 2019). As *S. frugiperda* expands its range across China, and even the globe, the potential for using native natural enemies is uncertain. Understanding the predation capacity of generalist predators native to the newly invaded regions will help us to guide management strategies for this invasive pest.

In this study, we evaluated the potential of *C. formosa* as a candidate biocontrol agent for managing *S. frugiperda* and *S. litura* by conducting functional response experiments, in which we used adult predator feeding on eggs and the first three instar larval stages of the prey. The predation capacity, functional response type and the parameters of *C. formosa* adult predation against each life stage of the prey were determined. We also compared the consumption ability and prey preference of *C. formosa* toward *S. frugiperda* and *S. litura* in one-prey and two-prey systems.

Materials and methods

Insect culture

A colony of the green lacewing, *C. formosa*, was maintained in the laboratory as described (Li et al., 2018). Larvae and adults of *C.*

formosa were all reared with abundant aphids, *Megoura japonica* (Matsumura), in a cage (60 cm in length, 60 cm in width and 60 cm in height) under conditions of $26 \pm 1^\circ\text{C}$, 16 h light/8 h dark (16L:8D) and $70 \pm 5\%$ relative humidity (RH). Adults that emerged on the same day were collected and cultured with aphids in a separate cage. *C. formosa* adults were then collected for functional responses, consumption of prey species and prey preference analysis 2–4 days after emergence.

The fall armyworm *S. frugiperda* was originally collected from maize fields in Chongming county (102.76°E , 25.12°N), Yunnan province, China, during May 2019. Eggs for the common cutworm *S. litura* were provided by the Jilin Academy of Agricultural Sciences. The first- to third-instar larvae of *S. frugiperda* were fed on an improved artificial diet (Greene et al., 1976), and *S. litura* larvae were also reared with specific artificial diets (Chen et al., 2021). These two species colonies were cultured in a climatic chamber at $26 \pm 1^\circ\text{C}$ and with 16L:8D and $70 \pm 5\%$ RH. Adults were fed with a 10% sucrose solution. In preliminary predation experiments, a single green lacewing *C. formosa* adult could consume *S. frugiperda* eggs, first and second-instar larvae and also could consume *S. litura* eggs and first-, second- and third-instar larvae. Therefore, eggs laid within 1 day and 1- to 2-day-old first and second-instar larvae of *S. frugiperda* and *S. litura* and 1-day-old third-instar larvae of *S. litura* were collected directly from the chambers for experimentation.

Experimental conditions

All experiments were performed under conditions of $26 \pm 1^\circ\text{C}$, 16L:8D and $70 \pm 5\%$ RH. Prior to each experiment, adults of *C. formosa* were starved for 24 h by keeping them individually in Petri dishes (6 cm in diameter). Each experimental arena (a Petri dish; 15 cm in diameter, 2.3 cm in height) contained a small piece of artificial diets to prevent cannibalism among the prey. After allocating the prey and predator, each Petri dish was covered and sealed with parafilm to prevent the prey from escaping.

C. formosa consumption of different prey species

To assess the ability of *C. formosa* to consume different prey species, 500 newly laid individual eggs, 200 first-instar larvae and 40 second-instar larvae of *S. frugiperda* and *S. litura* were offered separately to individual *C. formosa* adults. After 24 h, the number of individuals consumed was recorded by counting intact or living prey. For each prey life stage, 10–20 replicates were conducted.

Prey preference

To determine the relative preference of *C. formosa* for *S. frugiperda* and *S. litura*, a 24-h starved *C. formosa* adult and 50 first-instar larvae each of *S. frugiperda* and *S. litura* (for a total of 100 prey items) were transferred into an experimental arena. After 24 h, the number of prey consumed for each species was recorded. Because it is hard to distinguish eggs and the second-instar larvae of the two *Spodoptera* species morphologically, here we only studied the preference of *C. formosa* for first-instar larval prey. Sixteen adult females and males were used as replicates.

Determination of the functional responses

Prey densities to be offered were determined through preliminary tests to ensure that minimum and maximum levels of predation

would be obtained for each predator on each prey stage. Each 24-h starved female or male adult was exposed to five different densities of *S. frugiperda* or *S. litura* at different life stages (eggs and first-, second- and third-instar larvae). Prey densities offered to *C. formosa* adults are shown in table 1. Prey consumption was checked after a foraging period of 24 h, and the number of surviving prey individuals was recorded. In each treatment, 5–10 females and males (a total of 10–20 adults) were used as replicates for each prey density. Control treatments without predators were carried out and consisted of ten arenas for each prey density to determine the natural mortality by counting the dead prey.

Statistical analyses

There was no mortality for *S. frugiperda* or *S. litura* larvae in control groups, and thus prey mortality data did not have to be corrected in the experiments. A one-way analysis of variance (ANOVA) was performed to compare the amount and proportion of prey consumed by *C. formosa* at different prey densities. When significant differences were detected, the means were analyzed by Tukey’s multiple comparisons ($P < 0.05$). The consumption rates of *C. formosa* with respect to different life stages of *S. frugiperda* and *S. litura* at the highest prey densities were also compared by one-way ANOVA, followed by Tukey’s multiple comparisons ($P < 0.05$). Comparisons of prey consumption amount and prey preference of *C. formosa* for the two *Spodoptera* species were performed using the *t*-test. The prey preference was assessed by using Ivlev’s selectivity index (Lechowicz, 1982). The selectivity index $Ci = (Qi - Fi)/(Qi + Fi)$, in which Fi is the proportion of prey type i in the experimental system, Qi the proportion of prey type i consumed by the predator and Ci represents the preference of the predator for the prey type i . If $0 < Ci < 1$, there is a positive preference; if $-1 < Ci < 0$, there is a negative preference and $Ci = 0$ indicates no preference.

The type of functional response was determined by logistic regression of the proportion of prey consumed as a function of initial prey density, using a polynomial logistic regression fitted to the data:

$$N_e / N_0 = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}$$

where N_e is the number of prey consumed; N_0 is the initial prey density and P_0, P_1, P_2 and P_3 are the maximum likelihood estimates of the intercept, linear, quadratic and cubic coefficients, respectively (Juliano, 2001). The sign of the linear and quadratic coefficients is used to determine the type of functional response. If the linear coefficient (P_1) is not significantly different from 0, functional response is type I. If the linear coefficient is significantly negative (i.e., $P_1 < 0$), the predator displays a type II functional response. If the linear coefficient is positive (i.e., $P_1 > 0$) and the quadratic coefficient is negative (i.e., $P_2 < 0$), the predator displays a type III functional response (Juliano, 2001). The logistic regression analysis indicated that our data fit a type II functional response for *C. formosa* adults (table 2). Therefore, we used the random predator equation (Rogers, 1972), which allows for prey depletion, for estimation as below:

$$N_e = N_0 [1 - \exp(aT_h N_e - aT)]$$

in which N_e is the number of prey consumed, N_0 is the initial prey density, a is the attack rate, T is the searching time (1 day) and T_h

Table 1. Prey densities offered for functional responses of *C. formosa* adults to *S. frugiperda* and *S. litura*

Prey species	Life stage	Prey density ^a
<i>S. frugiperda</i>	Eggs	50, 100, 200, 300, 500
	First-instar larvae	30, 60, 90, 120, 200
	Second-instar larvae	5, 10, 15, 20, 40
<i>S. litura</i>	Eggs	50, 100, 200, 300, 500
	First-instar larvae	30, 50, 100, 150, 200
	Second-instar larvae	10, 20, 40, 60, 80
	Third-instar larvae	4, 8, 12, 20, 30

^aPrey densities are shown as the number of eggs or larvae per 15-cm dish.

is the handling time in days. These variables can also be used to calculate the maximum prey consumption, T/T_h . The extra sum-of-squares *F*-test was used to test for differences in the functional response attack rate and handling time between the two-prey species and among different prey stages. The functional response ratio ($FRR = a/T_h$) (Cuthbert *et al.*, 2019), which is used to predict the predation efficiency of the predator, was also calculated. Parameters were estimated using the non-linear least squares regression procedure. All data were analyzed using Prism 9.0 (GraphPad) and SigmaPlot (version 14, Systat Software, Inc.).

Results

Prey consumption

Adults of *C. formosa* exhibited high predation on the eggs and on the first two instar larval stages of *S. frugiperda* and *S. litura* when provided with individual prey species. When provided with the third-instar larvae of either prey, the green lacewing adult could only attack and kill *S. litura* successfully. In all cases, the number of prey consumed by *C. formosa* over a 24-h period increased significantly with the increase in prey densities and then attained a plateau when prey densities approached the upper asymptote (fig. 1). A larger variation in predation amounts was noted among predator individuals as prey densities increased. At the highest prey densities, the average daily consumption of *C. formosa* declined significantly with the development of the prey (table 3). For each prey species, the largest number of prey consumed was observed for eggs, followed by the first and second-instar larvae, respectively (table 3).

Prey species had no statistically significant effect with respect to consumption by *C. formosa* when the same number of eggs or first-instar larvae of *S. frugiperda* and *S. litura* was offered as prey in one-prey system (fig. 2). For *C. formosa* feeding on the second-instar larvae, there was a slight but significantly greater predation on *S. frugiperda* than on *S. litura* ($t = 2.666, df = 28, P = 0.0126$).

Prey preference

C. formosa adults consumed significantly larger numbers of first-instar larvae of *S. litura* than of *S. frugiperda*, regardless of the predator’s sex (female: $t = 2.418, df = 30, P = 0.0219$; male: $t = 2.463, df = 28, P = 0.0202$) (fig. 3a). Both female and male adults

Table 2. Parameters estimated from logistic regression analysis of the proportion of *S. frugiperda* and *S. litura* consumed by *C. formosa* adults as a function of initial prey density

Prey species and life stage	Type	Parameters	Estimate	SE	<i>t</i>	<i>P</i>
<i>S. frugiperda</i>	Eggs	P_0	1.1576	0.1327	8.7205	<0.0001
		P_1	-0.0048	0.0024	-1.9999	0.0519
		P_2	1.52×10^{-5}	1.07×10^{-5}	1.4177	0.1635
		P_3	-1.69×10^{-8}	1.31×10^{-8}	-1.2953	0.2021
	First-instar larvae	P_0	0.7133	0.0724	9.8451	<0.0001
		P_1	-0.0004	0.0028	-0.1582	0.8746
		P_2	-1.09×10^{-6}	2.98×10^{-5}	-0.0368	0.9707
		P_3	-2.39×10^{-8}	8.84×10^{-8}	-0.2699	0.7878
	Second-instar larvae	P_0	1.0560	0.0618	17.0882	<0.0001
		P_1	-0.0214	0.0138	-1.5543	0.1234
		P_2	0.0005	0.0008	0.6013	0.5491
		P_3	-7.56×10^{-6}	1.29×10^{-5}	-0.5876	0.5582
<i>S. litura</i>	Eggs	P_0	1.0425	0.0695	15.0065	<0.0001
		P_1	-0.0013	0.0013	-1.0415	0.3031
		P_2	-4.51×10^{-6}	5.71×10^{-6}	-0.7897	0.4338
		P_3	8.69×10^{-9}	6.99×10^{-9}	1.2435	0.2200
	First-instar larvae	P_0	1.1645	0.0887	13.1237	<0.0001
		P_1	-0.0078	0.0033	-2.3510	0.0231
		P_2	1.97×10^{-5}	3.26×10^{-5}	0.6046	0.5484
		P_3	7.86×10^{-10}	9.29×10^{-8}	0.0085	0.9933
	Second-instar larvae	P_0	1.0455	0.1043	10.0204	<0.0001
		P_1	-0.0302	0.0103	-2.9303	0.0053
		P_2	0.0005	0.0003	1.8685	0.0681
		P_3	-2.86×10^{-6}	1.91×10^{-6}	-1.5000	0.1404
	Third-instar larvae	P_0	1.0879	0.1322	8.2267	<0.0001
		P_1	-0.0703	0.0331	-2.1199	0.0378
		P_2	0.0025	0.0023	1.0954	0.2774
		P_3	-3.38×10^{-5}	4.46×10^{-5}	-0.7568	0.4519

showed a positive preference for the first-instar larvae of *S. litura* and displayed a negative preference for *S. frugiperda* at the same life stage (fig. 3b). There was no significant difference in the consumption rates between female and male adults of *C. formosa*.

Functional response

Type II functional responses were displayed by *C. formosa* adults toward each stage of *S. frugiperda* and *S. litura*, when they were offered separately, as evidenced by a significantly negative maximum likelihood estimate of the linear coefficient (i.e., $P_1 < 0$) (table 2) and decreased rates of consumption with increasing prey densities (figs 1, 4 and 5). The functional response data for *C. formosa* feeding on *S. frugiperda* or *S. litura* over a 24-h period fit the random predator equation well, also confirming a type II response for all prey life stages (table 4). The searching efficiency of *C. formosa*, as measured by the proportion of prey consumed, was higher at lower densities of all prey stages but declined significantly as the prey density increased (figs 4 and 5).

Attack rates and handling time of *C. formosa* varied depending on the life stage of the prey. The highest attack rate was observed for predators feeding on the second-instar larvae of *S. frugiperda* and eggs of *S. litura*. However, there was no significant difference among the attack rates estimated for different life stages of each prey type (table 4). In all cases, the handling time of *C. formosa* increased significantly as the prey developed from one growth stage to another. Prey species also had a distinct effect on functional response parameters, as reflected in the higher attack rate ($F_{(1, 176)} = 24.03, P < 0.0001$) and longer handling time ($F_{(1, 176)} = 9.186, P = 0.0028$) of *C. formosa* feeding on the second-instar larvae of *S. frugiperda* in contrast to *S. litura* second-instar larvae, whereas predators feeding on *S. frugiperda* eggs showed a shorter handling time in contrast to *S. litura* eggs ($F_{(1, 113)} = 9.12, P = 0.0031$) (table 4).

In many cases, the use of either attack rate (*a*) or handling time (T_h) alone would lead to contradictory predictions of predatory efficiency, and thus a new metric, the FRR (a/T_h) was proposed to resolve such contradictions (Cuthbert et al., 2019). High attack rate values and short-handling times should be associated with

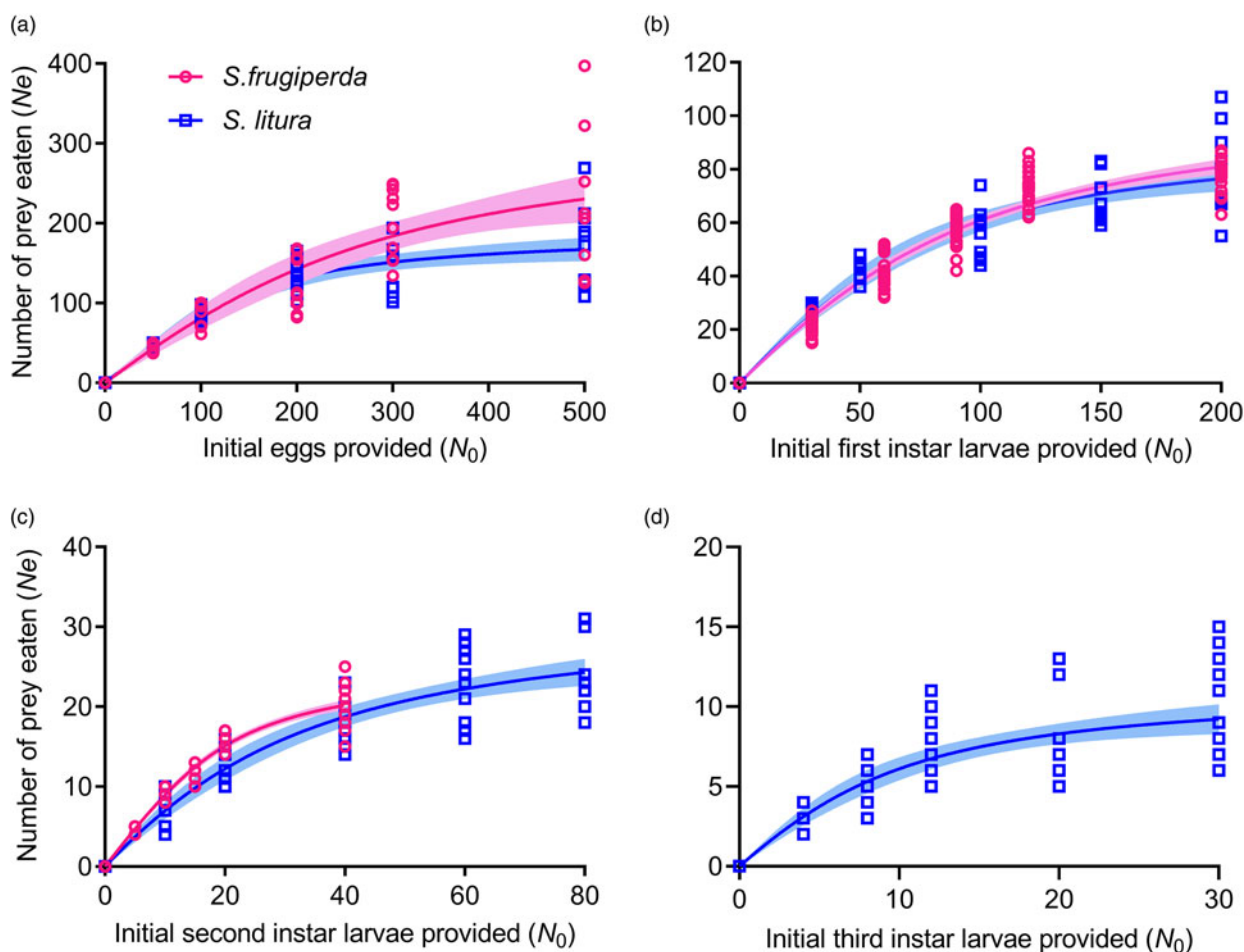


Figure 1. Functional response of *C. formosa* adults to different life stages of *S. frugiperda* and *S. litura*. (a–d) Prey consisted of eggs (a) and first (b), second (c) and third (d) instar larvae of *S. frugiperda* and *S. litura* at different densities as indicated. Data points represent the observed number of *S. frugiperda* and *S. litura* consumed at each initial prey density over a period of 24 h. Curves show predicted values based on Rogers random predator equation. Shaded areas indicate 95% confidence intervals.

high predation efficiency, and vice versa. *C. formosa* adults had the highest predation efficiency on eggs of each prey species (FRR = 705.3 for *S. frugiperda* eggs, FRR = 658.3 for *S. litura* eggs), followed by the first-instar larvae (table 4). The predation efficiency dropped notably with the development of the prey. When provided with eggs or second-instar larvae of the two-prey species separately, the *C. formosa* adults exhibited slightly higher predation efficiency on *S. frugiperda* than on *S. litura*, but when feeding on the first-instar larvae, *C. formosa* had similar predation efficiency for the two-prey species.

The theoretical maximum consumption (T/T_h) of *C. formosa* estimated according to handling time was close to the measured average daily consumption at the highest prey density, suggesting that parameters of functional response were reliable for predicting the predation ability of *C. formosa* (tables 3 and 4). This parameter also confirmed the results we obtained from a/T_h that the predation efficiency of *C. formosa* decreased with the development of the prey.

Discussion

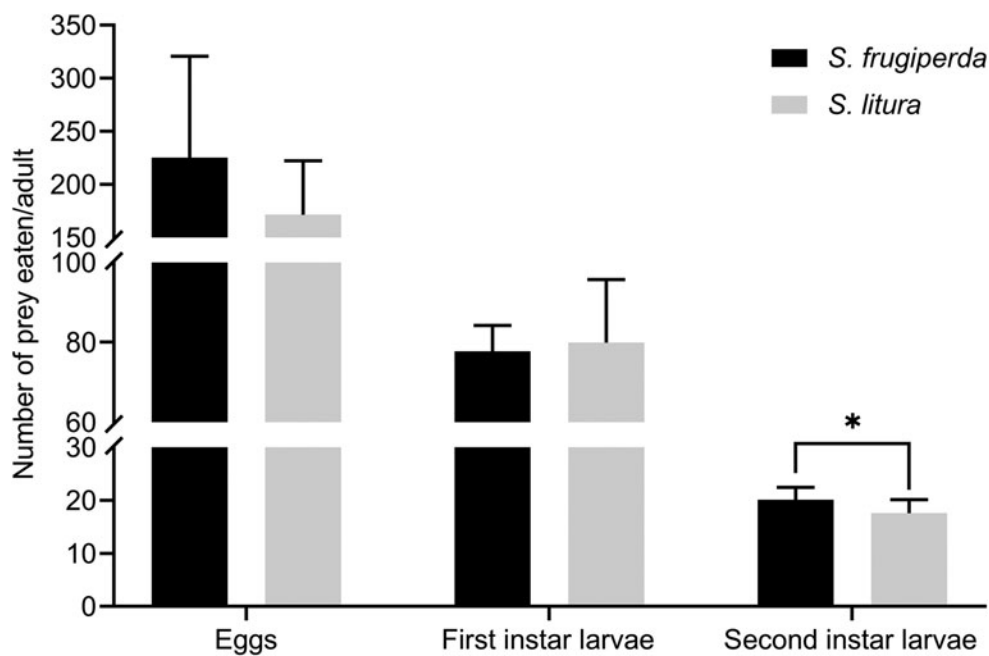
Our results indicated that the green lacewing, *C. formosa*, is a voracious predator of *Spodoptera* pests, with a high predation on eggs and earlier instar larvae of both *S. frugiperda* and *S. litura*. To our

knowledge, this is the first study to provide insights into the predation capacity and functional response of *C. formosa* adults on *S. frugiperda* and *S. litura*. The predation capacity of the chrysid toward eggs and the first two larval stages of *S. frugiperda* was relatively similar to its capacity toward those of *S. litura*. It was difficult for *C. formosa* adults to attack and kill the third-instar larvae of *S. frugiperda*, most likely because of their strong defensive behavior (Li *et al.*, 2020). We note, however, that adults of a larger chrysid species, *C. pallens*, can consume one to three third-instar larvae of *S. frugiperda* per day (Cao *et al.*, 2020). Larval stages of *C. formosa* also consume large numbers of eggs and young larvae of both *S. frugiperda* and *S. litura*, with the third-instar larval stage of *C. formosa* being the most voracious among these stages, as determined by our previous work (table 5) (Li *et al.*, 2021; Wang *et al.*, 2022). The maximum consumption of *C. formosa* adult against the first- and second-instar larvae of *S. frugiperda* is higher than that of adult *C. pallens* (Cao *et al.*, 2020), whereas the larval stages of *C. formosa* have lower predation than *C. pallens* larvae (Li *et al.*, 2020, 2021). Based on another study, *C. pallens* adults consume a larger number of *S. frugiperda* eggs than do *C. formosa* adults (table 5) (Xu *et al.*, 2019). Nunes *et al.* (2017) reported that the third-instar larvae of *Ceraeochrysa cubana* (Hagen) could consume 47.4 eggs and 63.5 newborn caterpillars of *S. frugiperda* daily, which is similar to consumption

Table 3. Prey consumption (\pm SD) per day for *C. formosa* adults with respect to different life stages of *S. frugiperda* and *S. litura* at the highest prey density

Prey life stage	<i>S. frugiperda</i>	<i>S. litura</i>
Eggs	225.3 \pm 95.53 a	171.7 \pm 50.72 a
First-instar larvae	77.9 \pm 6.35 b	79.9 \pm 15.84 b
Second-instar larvae	20.1 \pm 2.36 c	24.3 \pm 4.69 c
Third-instar larvae	N/A	9.4 \pm 3.1 c
	$F_{(2, 45)} = 83.56, P < 0.0001$	$F_{(3, 36)} = 76.37, P < 0.0001$

Each value represents the mean \pm SD ($n = 10-20$). Means within the same column followed by different lowercase letters were significantly different among different stages of prey consumed by *C. formosa* adults (one-way ANOVA followed by Tukey's multiple comparisons, $P < 0.01$).

**Figure 2.** Number of *S. frugiperda* and *S. litura* consumed by *C. formosa* adults in a one-prey system. *S. frugiperda* and *S. litura* were offered separately as prey at the same density and life stage. An asterisk indicates a significant difference based on a *t*-test.

by *C. formosa* (46.2 ± 8.9 eggs and 66.8 ± 13.3 first-instar larvae) (Li et al., 2021). When feeding on *S. litura* at similar stages, *C. formosa* adults also exhibited higher predation than other predators, such as *Harmonia axyridis* (Pallas) (Islam et al., 2020), *Cyrtopeltis tenuis* (Reuter) and *Harpactor fuscipes* (Fabricius) (Wang et al., 2022). These results indicate the potential use of *C. formosa* as an effective predator, with the adult stage and last instar larval stage having the most potential for biological control.

A steady decline in the predation efficiency of predators with the growth of the prey has been demonstrated in many chrysopids (Hassanpour et al., 2011; Tavares et al., 2011; Ganjisaffar and Perring, 2015; Qin et al., 2019). Similarly, the highest consumption and shortest-handling time was observed for adults of *C. formosa* feeding on eggs, followed by the first-instar larvae of both prey species. The higher predation of this chrysopid on eggs may be associated with their lower biomass and lack of defenses and with the easier handling of immobile eggs. In terms of nutrient requirements of the chrysopid, lepidopteran eggs and newborn caterpillars are generally considered as optimal prey for the development of lacewings (Huang and Enkegaard, 2010). Consistently, feeding with *S. frugiperda* eggs increases the survival

and reduces the larval and adult developmental time of the lacewing *C. cubana* (Nunes et al., 2017). *Chrysoperla externa* could successfully rear on *S. frugiperda* eggs and newly hatched larvae, but fails to develop from larvae to adults when fed with 1- to 2-day-old first-instar larvae of *S. frugiperda* (Tavares et al., 2011). The lower predation on *Spodoptera* larvae was probably a result of defensive behavior and more rapid movement with the increase in prey size, which made larvae more difficult to attack, subdue and consume, thus leading to rejection of the prey (Zanuncio et al., 2008). Our results indicate that the lacewing *C. formosa* will be an effective control agent early in an infestation when the two *Spodoptera* populations comprise more eggs and earlier instar larvae.

Feeding preference of polyphagous predators is one of the most important criteria used in the evaluation of their efficiency. As generalist predators that prey on many soft-bodied insects and mites, the consumption efficiency of the chrysopids is often influenced by prey preference and the presence of alternative prey (Pappas et al., 2007; Huang and Enkegaard, 2010; Tavares et al., 2011; Messelink et al., 2016). The current experiments provide evidence that *C. formosa* has a preference for *S. litura* relative

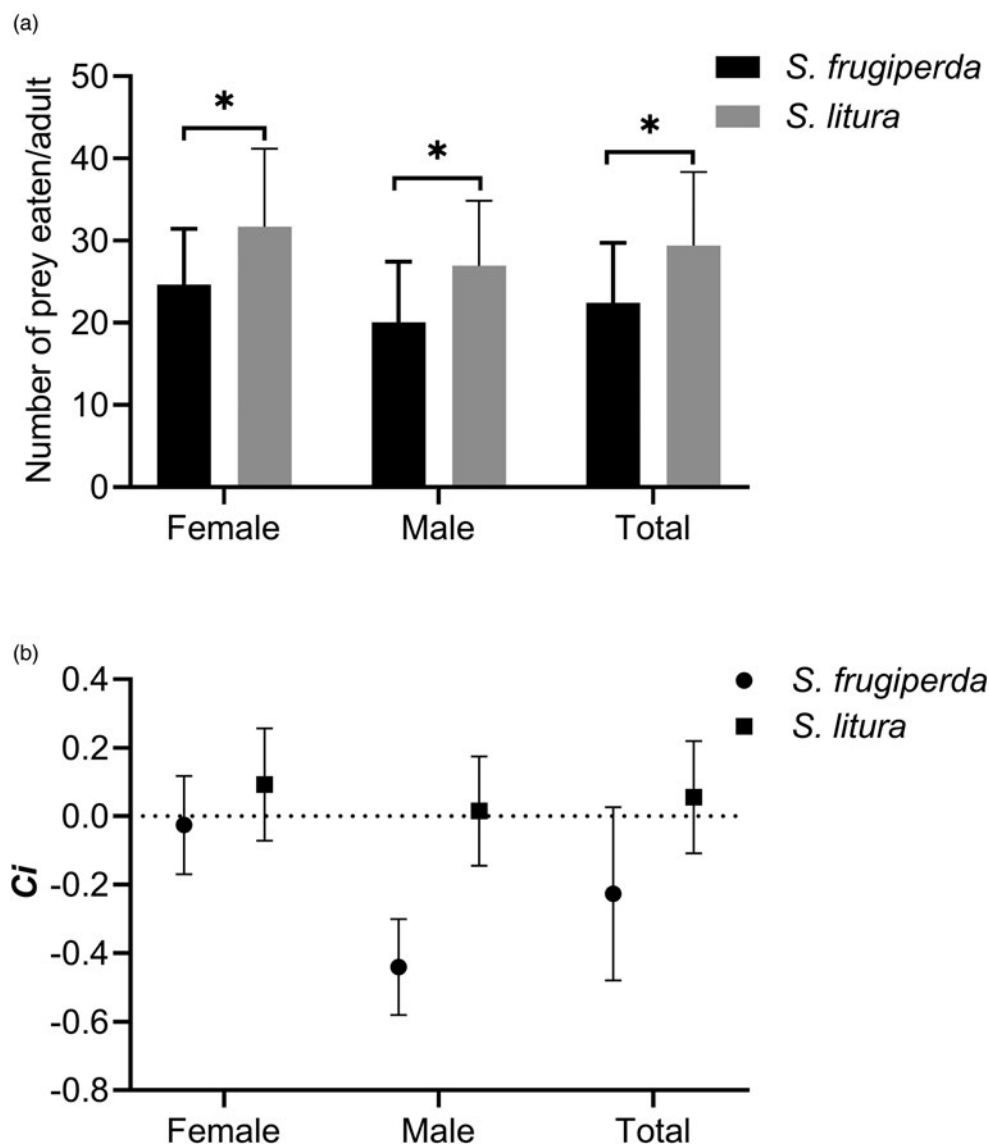


Figure 3. Mean consumption amount (a) and prey preference (C_i) (b) of *C. formosa* female and male adults feeding on *S. frugiperda* and *S. litura* in a two-prey system. An asterisk indicates a significant difference based on a *t*-test.

to *S. frugiperda* when both prey types are present, whereas their consumption rates were similar for this chrysopid species in a one-prey system. Preference of predators for different prey species often correlates with body size, nutrient quality and behavior traits of the prey (Pappas *et al.*, 2007; Huang and Enkegaard, 2010; Messelink *et al.*, 2016; Sattayawong *et al.*, 2016). A strong preference of *C. carnea* for aphids as compared with *Pieris brassicae* (Linnaeus) eggs might be a reflection of variation in nutritional quality (Huang and Enkegaard, 2010). Conversely, *Chrysoperla rufilabris* second- and third-instar larvae have a preference for the larger size of active caterpillars of *Heliothis virescens* (Fabricius) as compared with nymphs and adults of the cotton aphid *Aphis gossypii* Glover, but they prefer to feed on aphids over *H. virescens* eggs when offered the choice (Nordlund and Morrison, 1990). Among three cassava mealybug species, the higher preference of the green lacewing *Plesiochrysa ramburi* (Schneider) larvae for *Phenacoccus manihoti* (Matile-Ferrero) and *Phenacoccus madeirensis* (Green) relative to *Pseudococcus*

jackbeardsleyi (Gimpel & Miller) is probably due to the softer and smaller body size of the first two species (Sattayawong *et al.*, 2016). As the armyworms *S. frugiperda* and *S. litura* have very similar size and host ranges (Pogue, 2002; EPPO, 2015), we suspect that the higher degree of aggressiveness, stronger defenses and greater escape response of *S. frugiperda* larvae may lead *C. formosa* to reject that prey more frequently when alternatives are available (Li *et al.*, 2020). As evidenced by our observations, adults of *C. formosa* consumed 9.4 ± 3.1 third-instar larvae of *S. litura* daily but rarely attacked and fed on *S. frugiperda* third-instar larvae. Thus, caution must be taken when using this chrysopid to control *S. frugiperda* in the presence of *S. litura* in nature, because the functional response and predation efficiency may be affected by non-target prey species as supported by several studies (Nachappa *et al.*, 2006; Messelink *et al.*, 2016). The prey preference and predation efficiency of *C. formosa* in complex environments with multiple prey species should be further evaluated in the field.

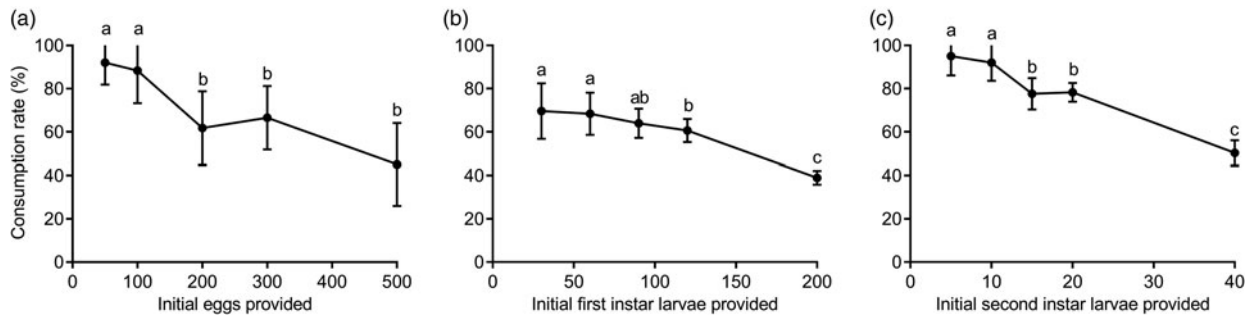


Figure 4. Proportion of *S. frugiperda* at different life stages consumed by *C. formosa* adults. (a–c) Consumption was assessed for *S. frugiperda* eggs (a) and first-instar (b) and second-instar (c) larvae when provided at the indicated densities. Values are the mean \pm SD ($n = 10\text{--}20$). Different letters indicate significant differences (Tukey's multiple comparisons, $P < 0.05$).

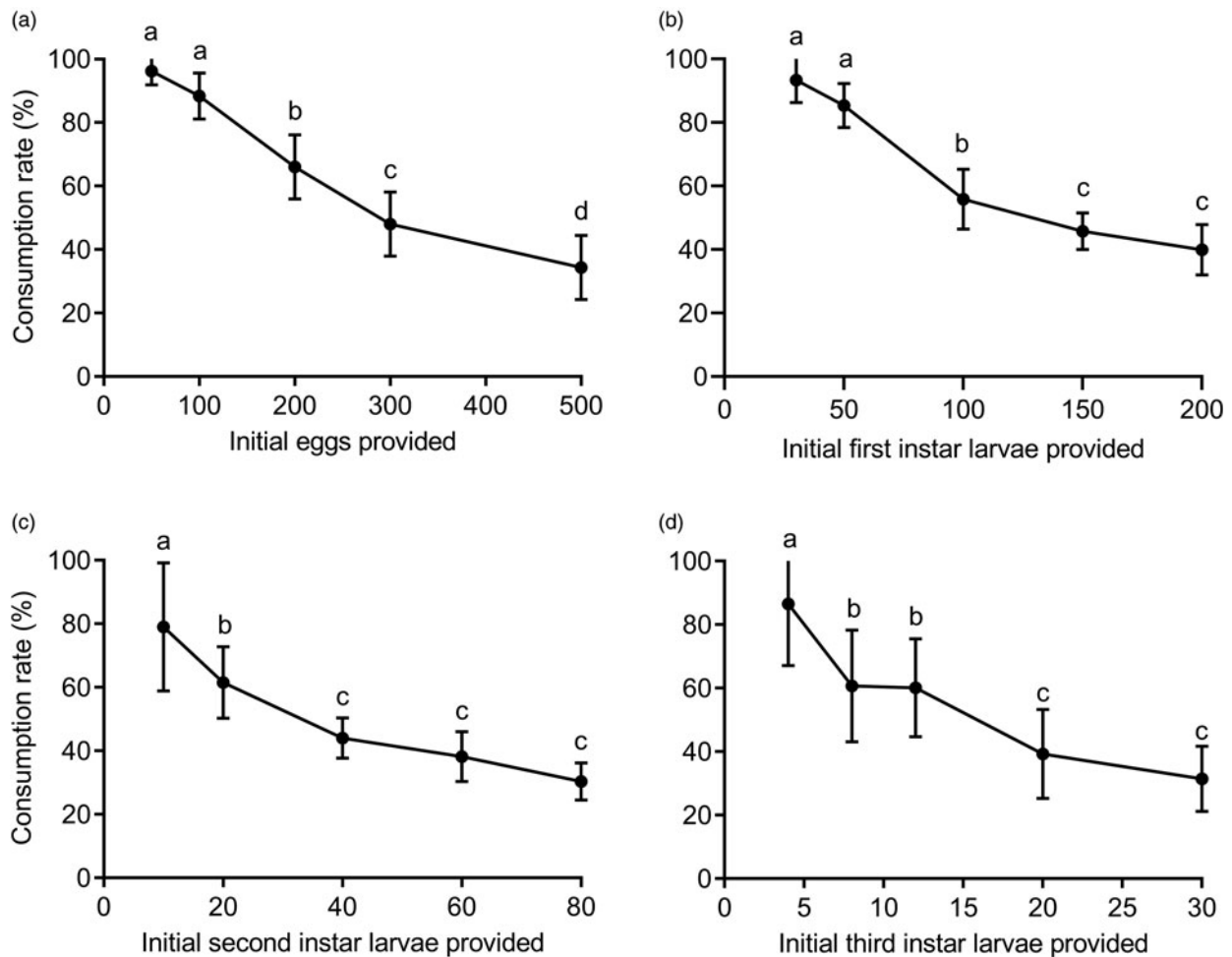


Figure 5. Proportion of *S. litura* at different life stages consumed by *C. formosa* adults. (a–d) Consumption was assessed for *S. litura* eggs (a) and first-instar (b), second-instar (c) and third-instar (d) larvae when provided at the indicated densities. Values are the mean \pm SD ($n = 10\text{--}20$). Different letters indicate significant differences (Tukey's multiple comparisons, $P < 0.05$).

C. formosa adults exhibited a type II functional response toward all prey stages for both prey species. A type II functional response is characterized by an inverse density-dependent relationship between the consumption rate and prey density, with the maximum consumption being limited by the handling time (Holling, 1965). This kind of functional response is commonly found among chrysopid species, including *C. pallens* (Cao *et al.*,

2020; Li *et al.*, 2020), *Chrysopa oculata* (Parajulee *et al.*, 2006), *C. sinica* (Huang *et al.*, 2020; Lai and Liu, 2020), *C. carnea* (Hassanpour *et al.*, 2011; Sultan and Khan, 2014), *C. rufilabris* (Stewart *et al.*, 2002) and *Ceraeochrysa caligata* (Viteri Jumbo *et al.*, 2019). However, type III functional responses can be observed for several chrysopids, such as the third-instar larvae of *C. carnea* feeding on *Helicoverpa armigera* (Hübner) eggs

Table 4. Parameter estimates (±SE) from the type II functional response of *C. formosa* adults preying on different life stages of *S. frugiperda* and *S. litura*

Prey species and life stage	Attack rate (a)	95% confidence interval (CI)	Handling time (T_h , in days)	95% CI	Maximum consumption (T/T_h)	FRR (a/T_h)	R^2	$P > F$
<i>S. frugiperda</i>								
Eggs	2.257 ± 0.6561	1.357–4.391	0.0032 ± 0.0006 c [†]	0.0020–0.0042	312.5	705.3	0.7731	<0.0001
First-instar larvae	2.216 ± 0.1647	1.931–2.569	0.0095 ± 0.0004 b	0.0087–0.0102	105.3	233.3	0.9533	<0.0001
Second-instar larvae	3.468 ± 0.2534 [†]	3.020–4.027	0.0395 ± 0.0012 a [§]	0.0371–0.0419	25.3	87.8	0.9670	<0.0001
$F_{(2, 291)} = 0.095,$ $P = 0.9098$			$F_{(2, 291)} = 13.94,$ $P < 0.0001$					
<i>S. litura</i>								
Eggs	3.489 ± 0.9588	2.153–7.264	0.0053 ± 0.0004 d [†]	0.0045–0.0061	188.7	658.3	0.8508	<0.0001
First-instar larvae	2.602 ± 0.4788	1.831–3.997	0.0107 ± 0.0007 c	0.0091–0.0122	93.5	243.2	0.9035	<0.0001
Second-instar larvae	1.534 ± 0.2597 [†]	1.108–2.219	0.0314 ± 0.0026 b [§]	0.0258–0.0366	31.8	48.9	0.8840	<0.0001
Third-instar larvae	2.074 ± 0.5010	1.333–3.598	0.0894 ± 0.0087a	0.0714–0.1067	11.2	23.2	0.7203	<0.0001
$F_{(3, 255)} = 0.575, P = 0.6321$			$F_{(3, 255)} = 7.148,$ $P = 0.0001$					

Values in the same column for an individual prey species followed by different lowercase letters are significantly different as determined by the extra sum-of-squares F-test. ^{†, ‡, §}The same symbols indicate significant differences for estimated parameters a and T_h between the same stage of the two-prey species (extra sum-of-squares F-test).

(Hassanpour *et al.*, 2011) and sugar cane whitefly *Aleurolobus barodensis* (Maskell) (Sultan and Khan, 2014), the third-instar larvae of *Chrysoperla congrua* on *H. armigera* eggs (Kabissa *et al.*, 1996) and the second-instar larvae of *C. caligata* preying upon red palm mite *Raoiella indica* (Hirst) (Viteri Jumbo *et al.*, 2019). Although predators with type II functional responses are considered less efficient than those with type III responses in long-term suppression of prey populations (Holling, 1965), the chrysopids with a type II response can be more effective at lower prey densities and thus used for augmentative biological control. In addition to prey species and size, the predation efficiency of a predator also could be influenced by the numerical response of a group of predators (Mushtaq and Khan, 2010), the hunger level of a predator (Hassanpour *et al.*, 2015; Pan *et al.*, 2019), intraguild predation (Noppe *et al.*, 2012), prey distribution (Feng *et al.*, 2018), host plants (Barbosa *et al.*, 2019) and abiotic environmental factors (Parajulee *et al.*, 2006; Ziaei Madbouni *et al.*, 2017). Under complex environmental conditions in the field, the predator could exhibit a type III functional response caused by the growth of its body size (Viteri Jumbo *et al.*, 2019), prey switching (Schenk and Bacher, 2002) or the size of the search area (Feng *et al.*, 2018). To improve their biological control efficiency, chrysopids with a type II functional response would need to be released early and at a high predator-prey ratio in an augmentative biological control program.

Attack rate and handling time are valuable indicators of predation ability, as they determine the capture success and the cumulative time invested in capturing, killing and digesting the prey (Viteri Jumbo *et al.*, 2019). The two parameters may be affected by many factors, such as prey species, stage, movement and defense behaviors (Hassell, 1978; Ganjisaffar and Perring, 2015), as well as predator stage, food preference, voracity, walking speed and digesting rate (Hassanpour *et al.*, 2011). Based on our observations, prey stage had a distinct influence on the handling time of *C. formosa* for both prey species, whereas no statistically significant difference was noted for the attack rate. The attack rate and handling time of *C. formosa* showed a life stage-dependent difference between the two-prey species. Based on a/T_h , *C. formosa* adults exhibited a greater predation efficiency on eggs and second-instar larvae of *S. frugiperda* than that of *S. litura*, which suggests that this chrysopid may be more efficient in controlling the invasive *S. frugiperda*.

The functional response of chrysopids on noctuid pests, including *S. frugiperda* (Xu *et al.*, 2019; Cao *et al.*, 2020; Huang *et al.*, 2020; Li *et al.*, 2021), *S. litura* (Wang *et al.*, 2022), *H. armigera* (Huang *et al.*, 1990; Hassanpour *et al.*, 2011), *H. virescens* (Hernández-Juárez *et al.*, 2015) and *Helicoverpa zea* (Boddie) (Parajulee *et al.*, 2006) has been reported in several studies. As shown in table 5, we summarize the functional response type, the estimated attack rate, handling time and predation efficiency (a/T_h) for these lacewing species and compare these values with those obtained for *C. formosa*. Most chrysopids showed a type II response against different stages of noctuid pests, with the exception of the third-instar larvae of *C. carnea* and *C. congrua* (table 5). It is obvious that the functional response parameters are generally varied for different species and stages of both prey and predator, which indicates that predators exhibiting analogous functional response curves cannot be deemed to respond similarly. As is common, but not universal (Stewart *et al.*, 2002; Viteri Jumbo *et al.*, 2019), the consumption ability and attack rate of predators usually increase, but the handling time decreases as they develop (Lee and Kang, 2004; Huang and Enkegaard,

Table 5. Summary of recent studies on the functional response of chrysopid species to noctuid pests

Prey species and life stage	Chrysopid species	Chrysopid life stage	Type of response	Attack rate (<i>a</i>)	Handling time (<i>T_h</i> , in days)	Predation efficiency (<i>a/T_h</i>)	Reference	
<i>S. frugiperda</i> egg	<i>C. formosa</i>	Second-instar larva	II	1.744	0.0315 ^a	55.4	Li <i>et al.</i> (2021)	
		Third-instar larva	II	1.579	0.0199 ^a	79.3	Li <i>et al.</i> (2021)	
		Adult	II	2.257	0.0032	705.3	Present study	
	<i>C. pallens</i>	Adult	II	1.004	0.0009	1115.56	Xu <i>et al.</i> (2019)	
	<i>C. sinica</i>	First-instar larva	II	0.345	0.014	24.160	Huang <i>et al.</i> (2020)	
		Second-instar larva	II	0.993	0.016	62.456	Huang <i>et al.</i> (2020)	
		Third-instar larva	II	1.016	0.005	195.494	Huang <i>et al.</i> (2020)	
	<i>C. carnea</i>	First-instar larva	II	0.62	0.13	4.77 ^b	Hernández-Juárez <i>et al.</i> (2015)	
		Second-instar larva	II	1.01	0.02	50.5 ^b	Hernández-Juárez <i>et al.</i> (2015)	
Third-instar larva		II	0.94	0.002	470 ^b	Hernández-Juárez <i>et al.</i> (2015)		
<i>S. frugiperda</i> first-instar larva	<i>C. formosa</i>	Second-instar larva	II	1.731	0.0483 ^a	35.8	Li <i>et al.</i> (2021)	
		Third-instar larva	II	1.032	0.011 ^a	93.8	Li <i>et al.</i> (2021)	
		Adult	II	2.216	0.0095	233.3	Present study	
	<i>C. pallens</i>	Second-instar larva	II	1.222	0.008	152.75	Li <i>et al.</i> (2020)	
		Third-instar larva	II	1.148	0.006	191.333	Li <i>et al.</i> (2020)	
		Third-instar larva	II	1.074	0.003	358	Xu <i>et al.</i> (2019)	
		Adult	II	0.519	0.073	7.156	Xu <i>et al.</i> (2019)	
	<i>C. sinica</i>	Adult	II	1.023	0.070	14.61	Cao <i>et al.</i> (2020)	
		First-instar larva	II	0.660	0.017	37.917	Huang <i>et al.</i> (2020)	
		Second-instar larva	II	0.699	0.012	59.234	Huang <i>et al.</i> (2020)	
	<i>S. frugiperda</i> second-instar larva	<i>C. formosa</i>	Third-instar larva	II	0.889	0.006	148.227	Huang <i>et al.</i> (2020)
			Adult	II	1.111	0.039 ^a	28.5	Li <i>et al.</i> (2021)
<i>C. pallens</i>		Second-instar larva	II	3.468	0.0395	87.8	Present study	
		Third-instar larva	II	0.870	0.046	18.913	Li <i>et al.</i> (2020)	
<i>C. sinica</i>		Third-instar larva	II	1.305	0.031	42.097	Li <i>et al.</i> (2020)	
		Adult	II	0.618	0.097	6.37	Cao <i>et al.</i> (2020)	
<i>S. frugiperda</i> third-instar larva	<i>C. sinica</i>	Second-instar larva	II	0.472	0.037	12.402	Huang <i>et al.</i> (2020)	
		Third-instar larva	II	0.825	0.014	60.648	Huang <i>et al.</i> (2020)	
<i>S. frugiperda</i> third-instar larva	<i>C. pallens</i>	Adult	II	0.313	0.305	1.03	Cao <i>et al.</i> (2020)	
<i>S. litura</i> egg	<i>C. formosa</i>	Third-instar larva	II	1.801	0.0032 ^a	562.8 ^b	Wang <i>et al.</i> (2022)	
		Adult	II	3.489	0.0053	658.3	Present study	

(Continued)

Table 5. (Continued.)

Prey species and life stage	Chrysopid species	Chrysopid life stage	Type of response	Attack rate (a)	Handling time (T_h , in days)	Predation efficiency (a/T_h)	Reference
<i>S. litura</i> first-instar larva	<i>C. formosa</i>	THIRD-instar larva	II	1.835	0.0077 ^a	238.3 ^b	Wang <i>et al.</i> (2022)
		Adult	II	2.602	0.0107	243.2	Present study
<i>S. litura</i> second-instar larva	<i>C. formosa</i>	Third-instar larva	II	1.542	0.0301 ^a	51.2 ^b	Wang <i>et al.</i> (2022)
		Adult	II	1.534	0.0314	48.9	Present study
<i>S. litura</i> third-instar larva	<i>C. formosa</i>	Third-instar larva	II	1.204	0.0657 ^a	18.3 ^b	Wang <i>et al.</i> (2022)
		Adult	II	2.074	0.0894	23.2	Present study
<i>H. armigera</i> egg	<i>C. carnea</i>	First-instar larva	II	0.590	0.0287 ^a	20.6 ^b	Hassanpour <i>et al.</i> (2011)
		Second-instar larva	II	0.407	0.0069 ^a	58.99 ^b	Hassanpour <i>et al.</i> (2011)
		Third-instar larva	III	0.036	0.00296 ^a	N/A	Hassanpour <i>et al.</i> (2011)
<i>H. armigera</i> first-instar larva	<i>C. carnea</i>	First-instar larva	II	0.294	0.0297 ^a	9.9 ^b	Hassanpour <i>et al.</i> (2011)
		Second-instar larva	II	0.858	0.0094 ^a	91.3 ^b	Hassanpour <i>et al.</i> (2011)
		Third-instar larva	II	1.015	0.0036 ^a	281.9 ^b	Hassanpour <i>et al.</i> (2011)
	<i>Mallada desjardinsi</i>	Third-instar larva	II	0.044	0.00108 ^a	40.7 ^b	Kabissa <i>et al.</i> (1996)
	<i>C. congrua</i>	Third-instar larva	III	0.050	0.0017 ^a	N/A	Kabissa <i>et al.</i> (1996)
<i>H. zea</i> egg	<i>C. oculata</i>	Third-instar larva	II	0.220	0.0127 ^a	17.3 ^b	Parajulee <i>et al.</i> (2006)
<i>H. virescens</i> egg	<i>C. carnea</i>	First-instar larva	II	0.89	0.15	5.9 ^b	Hernández-Juárez <i>et al.</i> (2015)
		Second-instar larva	II	0.99	0.02	49.5 ^b	Hernández-Juárez <i>et al.</i> (2015)
		Third-instar larva	II	1.03	0.002	515 ^b	Hernández-Juárez <i>et al.</i> (2015)

^aTo facilitate comparisons, the handling time was converted to days.

^bValues were calculated based on the data presented in the references.

2010; Li et al., 2021). The adult and final instar stages of lacewing larvae generally are associated with a higher level of predation efficiency relative to earlier stages. Although there were some differences in the experimental conditions, such as the experimental arena size, duration and temperature and statistical method used in these studies (Kabissa et al., 1996; Parajulee et al., 2006; Hassanpour et al., 2011; Xu et al., 2019), *C. formosa* adults and larval stages seem to have a relatively higher or similar predation efficiency when compared with the same stage of other chrysopid species. Currently, the most commonly used commercially available lacewings are *Chrysoperla* species, including *C. carnea*, *C. sinica*, *C. rufilabris* and *Chrysoperla comanche* (Banks), which exhibit their predation capacity only as larvae (Pappas et al., 2011). The great ability of *C. formosa* to consume prey as larvae and as adults may be an important advantage for their use in biological control.

Despite the limitations of a laboratory-determined functional response, the results presented here demonstrate that *C. formosa* is a promising agent for biological control of both *S. frugiperda* and *S. litura*. The most suitable time to introduce the chrysopid in augmentative biological control is when the prey population at lower densities and consists of more eggs and first- to second-instar larvae relative to later life stages. The findings can help us to understand the ecological mechanisms of predator-prey interactions in the field. However, to develop a biological control program for *Spodoptera* pests using *C. formosa*, further experiments into the foraging ability, developmental performance, prey preference, numerical response and release methods of *C. formosa* should be conducted under both laboratory and field conditions.

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