Biological Control 50 (2009) 25–29

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Predation by *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) on *Myzus persicae* Sulzer (Homoptera: Aphididae): Effect of prey density

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ARTICLE INFO

Article history:
Received 24 October 2008
Accepted 22 January 2009
Available online 7 February 2009

Keywords:
Functional response
Voracity
Biological control
Coccinella undecimpunctata
Myzus persicae

ABSTRACT

To enhance a strategy for the biological control of *Myzus persicae* Sulzer (Homoptera: Aphididae) using *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae), it is important to understand predator–prey interactions. Hence, the voracity and functional response of 4th instar larvae and adults (males and females) of *C. undecimpunctata* L. on *Myzus persicae* Sulzer were evaluated under laboratory conditions. This study took place in small plastic boxes at varying aphid densities. Satiation was attained when 130 aphids were provided to 4th instar larvae and 90 to adult males or females. *Coccinella undecimpunctata* exhibited a type II functional response; fourth instar larvae displayed a lower handling time than adults and attack rates were similar between larvae and adults and, between females and males (i.e., not sex-dependent). *Coccinella undecimpunctata* showed to be an effective predator for the biological control of *M. persicae* under controlled conditions, and it is hypothesized that the presence of both 4th instar larvae and adults of this ladybird beetle could increase the efficiency on field pest suppression.

1. Introduction

Numerical interactions between predators and their prey are frequently cyclical in nature because of delays in the reproductive response of the predator. What happens, in effect, is that each predator is able to catch more food as the prey becomes more abundant and this food is converted, after a certain period, into more predators. This primary feeding response of the predator is usually termed functional response, which is actually recognized as an intrinsic part of the prey's density-dependence regulating mechanism (Mills, 1982; Berryman and Kindlmann, 2008). There are three basic types of functional responses but all of them have a single common property: the number of prey eaten per predator per unit of time increases with prey density until predators become satiated (Berryman and Kindlmann, 2008). The functional response curves can be characterized and differentiated by evaluating the coefficients of attack rate and handling time (time spent by the predator in subduing and eating the prey). The coefficient of attack rate estimates the steepness of the increase in predation with increasing prey density and handling time helps estimate the satiation threshold (Pervez and Omkar, 2005). Several types of functional response have been described, including a linear increase (Type I), an increase decelerating to a plateau (Type II) or a sigmoid increase (Type III) resulting in a constant (I), decreasing (II) and increasing (III) rate of prey killing (Hassell et al., 1977; Hodek and Honěk, 1996; Pervez and Omkar, 2005). Given that such curves describe the rate at which a predator kills its prey at different prey densities, they are also useful tools for the determination of the efficiency of a predator in regulating prey populations, and thus to forecast the predator's effectiveness as a biological control agent (Deligeorgidis et al., 2005; Pervez and Omkar, 2005; Sarmento et al., 2007).

Aphid populations can become very abundant over time and space (Kindlmann and Dixon, 1993; Dixon, 1998; Borges et al., 2006) and, predators, as aphidophagous coccinellids, can react in many ways to the changes in prey density. From a practical point of view, the knowledge of the functional response may provide useful information about the potential efficacy of these predators as biological control agents.

Aphidophagous ladybird beetles are important predators of aphids in agricultural crops, and have been receiving attention as biological control agents due to some of their characteristics, such as: ability to feed on a wide range of prey, to be very voracious and to have a rapid numeric response (Hodek and Honěk, 1996; Obrycki and Kring, 1998; Dixon, 2000). *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) is a euriphagous predator, which prefers to feed on aphids (Raimundo and Alves, 1986; Hodek and Honěk, 1996). According to Soares et al. (2003b), this ladybird beetle is established in the Azores and has potential to be a biological control agent against aphids.

The green peach aphid, *Myzus persicae* Sulzer (Homoptera: Aphididae) is considered one major pest in Azorean agricultural systems, causing serious damage to horticulture, both in fields and

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doi:10.1016/j.biocontrol.2009.01.020

greenhouses. This pest is also found worldwide threatening many economically important plants (horticultural to ornamental), mainly due to the transmission of plant viruses (Minks and Harrewijn, 1989; Blackman and Eastop, 2000). A recent study showed that *M. persicae*, from an ecophysiological point of view, is an essential prey to *C. undecimpunctata*, allowing the predator's complete development and reproduction (Cabral et al., 2006). However, to enhance a strategy for the biological control of *M. persicae* using *C. undecimpunctata*, it is important to understand predator–prey interactions, namely predator functional response (Holling, 1959; Mills, 1982; Omkar and Pervez, 2004). Therefore, in this study we (i) evaluated the effect density of *M. persicae* on the voracity of adults (males and females) and 4th instar larvae of *C. undecimpunctata* and, (ii) characterized the functional response of *C. undecimpunctata* (i.e., the shape and the coefficients of attack rate and handling time of the response curves).

2. Material and methods

2.1. Insects

Adults of *C. undecimpunctata* were collected in Sta. Maria Island, Azores, Portugal, early in the summer (July, 2006) before experiments took place. Ladybird beetles were reared in cages (50 × 50 × 50 cm) covered by mesh, at 25 ± 1 °C, 75 ± 5% RH and a photoperiod of 16L:8D, using fluorescent lamps (Sylvania Standard F36 W/133). Insects were provided with an *ad libitum* mixed diet of different developmental stages of aphids [*Aphis fabae* (Scopoli) and *M. persicae* (Homoptera: Aphididae) reared on *Vicia faba major* L.], multiflower bee pollen and a solution of honey diluted in water (30%) applied to cotton. Individuals (4th instar larvae and adults) produced in this rearing system were used for experiments.

2.2. Voracity

Prior to the experiments, larvae and adults were held in separate Petri dishes (3 cm in depth and 5 cm in diameter) and fed *ad libitum* with the mixed diet. Larvae were maintained under these conditions for 12 h after moulting to the 4th instar, while adults were equally maintained during 12–24 h after their emergence.

Voracity of 4th instar and adults (males and females) during sexual maturation period was evaluated on single diets of *M. persicae*. Each individual of the 4th instar, female or male ladybird beetle was provided with one of the following prey densities: 10, 30, 50, 70, 90, 110, 130, 150 or 170 nymphs of the last developmental stage and apterous females of *M. persicae*. After 24 h the number of surviving prey was recorded in each treatment. All treatments were performed at 25 ± 1 °C, 75 ± 5% RH and a photoperiod of 16L:8D under fluorescent lamps (Sylvania Standard F36 W/133). In order to evaluate the ratio of natural mortality of prey, control treatments were performed with the above-mentioned prey densities, but in the absence of predators. Abiotic conditions were the same as previously mentioned. Ten replicates for each treatment were carried out. Voracity (V_o) was determined according to the following equation (Soares et al., 2003a):

$$V_o = (A - a_{24})ra_{24}$$

where V_o is the number of aphids eaten, A is the number of aphids available, a_{24} is the number of aphids alive after 24 h and ra_{24} is the ratio of aphids alive after 24 h in the control treatment.

2.3. Functional response

Data were fit to the "random-predator" equation (Rogers, 1972), a modification of Holling's (1959) disk equation, that is regarded as more appropriate because it considers prey density to be affected by prey consumption (Hazzard and Ferro, 1991):

$$N_a/TP = \alpha N/(1 + \alpha T_h N)$$

where N_a is the number of prey attacked, T is the total time of prey exposure, P is the number of predators, N is the initial prey density, α is the attack rate (or searching efficiency) and T_h is the handling time (i.e., the time spent handling each prey attacked). In this experiment, $T = P = 1$, because prey were exposed to one predator for 1 day. The parameters α and T_h were estimated using the number of aphids consumed as dependent variable.

2.4. Statistical analysis

One-factor ANOVA was used to compare the voracity of *C. undecimpunctata* under different prey densities and the voracity of larvae, females and males at each prey density. When ANOVA showed significant differences ($P < 0.05$) among data sets, paired comparisons of each mean were made using Fisher's protected LSD tests (Zar, 1996). All analyses were performed using SPSS v. 12.0 for Windows (SPSS, Inc., 2004). Functional response model parameters were calculated and the curve was plotted for untransformed data, using the nonlinear regression module of SPSS v. 12.0 for Windows (SPSS, Inc., 2004). Significance of the regression model was evaluated by ANOVA and the variance explained by the model was expressed by the coefficient of determination.

3. Results

3.1. Voracity

The number of prey eaten by 4th instar larvae of *C. undecimpunctata* increased significantly with prey density, reaching the maximum value when 130 prey were provided (i.e., 47.21 ± 1.38 prey were consumed). Voracity of males and females also increased significantly with prey density, but for adults satiation was attained at a lower prey density, that is, when 90 prey were provided (i.e., 39.85 ± 0.63 and 39.02 ± 1.42 prey were consumed, respectively) (Table 1). Voracity did not differ between developmental stages, except for prey densities of 90 and 130 aphids (Table 1).

3.2. Functional response

Voracity data fitted to the modified Holling (1959) disk equation showed that the number of prey consumed during 24 h increased with prey density at a monotonic decelerating rate, representing a typical type II response (Fig. 1). Estimated models accounted for a significant portion of the initial variance of the data

Table 1
Voracity (number of prey eaten ± SE) of *C. undecimpunctata* 4th instar larvae and adults (females and males) fed on different densities (number of prey provided) of *M. persicae*.

Prey density	Voracity ± SE		
	Larvae (4th instar)	Adult females	Adult males
10	8.0 ± 0.00a	8.0 ± 0.00a	8.0 ± 0.00a
30	18.6 ± 0.00b	18.6 ± 0.00b	18.6 ± 0.00b
50	23.5 ± 0.05c	23.4 ± 0.94c	22.7 ± 0.50c
70	34.6 ± 0.64d	32.6 ± 1.16d	32.1 ± 0.93d
90	39.9 ± 0.63e	39.0 ± 1.42e	34.2 ± 1.90de*
110	38.0 ± 1.25e	39.8 ± 1.18e	36.5 ± 1.53e
130	47.2 ± 1.38f*	38.8 ± 1.24e	36.4 ± 1.53e
150	48.3 ± 1.10f	–	–
170	48.8 ± 1.77f	–	–

Means within a column followed by different letters and means within a row followed by an asterisk (*) are significantly different at $P < 0.05$ (LSD test).

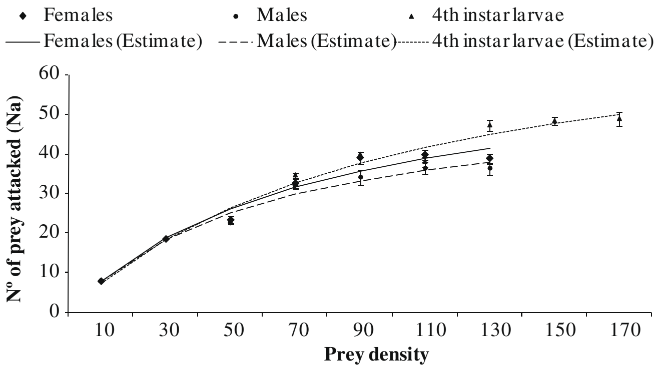

Fig. 1. Functional response [data fitted to "random predator" equation (Rogers, 1972)] of *C. undecimpunctata* 4th instar larvae and adults (females and males) fed on different prey densities of *M. persicae* during 24 h.

for voracity of 4th instar larvae and female and male adults (Table 2).

Results showed that (i) 4th instar larvae displayed a lower handling time (T_h) than adults (significantly different from males), (ii) attack rates were similar between 4th instar larvae and adults and, between females and males (i.e., not sex-dependent) (Table 2).

4. Discussion

Our results showed that *C. undecimpunctata* was able to eat a large amount of individuals of *M. persicae*, mainly for densities below the maximum voracity levels (i.e., 90 aphids for adults and 130 aphids for 4th instar larvae). Comparing with other coccinellids, such as *Coccinella transversalis* Fabricius (Omkar and James, 2004), *Hipopodemia convergens* Guerin-Meneville and *Coccinella septempunctata* L. (Omkar and Srivastava, 2003; Katsarou et al., 2005), all preying on *M. persicae*, *C. undecimpunctata* presents much higher voracity values. Fourth instar larvae were more voracious than adult males and females, as observed in previous studies by Cabral et al. (2006) and Moura et al. (2006). The higher voracity of 4th instar larvae is also frequently observed in other coccinellid species [e.g., *C. transversalis* (Omkar and James, 2004), *Propylea dissecta* Mulsant (Omkar and Pervez, 2004), *Harmonia axyridis* Pallas (Lee and Kang, 2004)] and is possibly due to the high requirements of energy intake for growth and to attain critical weight for pupation (Hodek and Honěk, 1996).

Coccinellid adult females usually are more voracious than males, owing to their larger size and high requirements of nutrients for egg production and oviposition (Hodek and Honěk, 1996; Lucas et al., 1997; Omkar and Pervez, 2004; Evans and Gunther, 2005); however, our results do not entirely accord with the findings reported by these authors, since the voracity of adult females and males of *C. undecimpunctata* was generally similar. In our case, such result could be due to the use of different prey instar with varying body sizes (i.e., nymphs of the 4th instar and adult females), as previously hypothesized by Moura et al. (2006). Under such conditions, and due to the smaller size of the males, it should be more advantageous for them to catch smaller prey even if larger ones offer a higher energetic gain, since capture success generally decreases with increasing prey size (Hassel et al., 1976, Roger et al., 2000; Soares et al., 2004). Another possible explanation is that the females used in the experiments were not laying eggs and thus were not requiring maximum food intake to produce and lay eggs; however, *C. undecimpunctata* females used on the experiments by Moura et al. (2006) were already sexually mature and still the voracity did not differ between the sexes.

Although the three types of functional responses described by Holling (1959) may occur in coccinellids (Hodek and Honěk, 1996), the fact is that type II is the most common in this group, as reported for several ladybird beetles preying on distinct aphid species, such as *Cheilomenes vicina* Mulsant (Ofuya, 1986), *C. septempunctata* (Kumar et al., 1999), *Scymnus creperus* Mulsant (Wells et al., 2001), *H. axyridis* (Lee and Kang, 2004), *P. dissecta* (Omkar and Pervez, 2004; Pervez and Omkar, 2005), *Cheilomenes sexmaculata* Fabricius and *C. transversalis* (Pervez and Omkar, 2005). *Coccinella undecimpunctata* also exhibited a type II functional response (Fig. 1), i.e., a convex curve that represents a decelerating increase in the number of consumed prey with increasing prey density until a plateau is reached (Ferran and Dixon, 1993). Similarly, Moura et al. (2006) observed this type of response of *C. undecimpunctata* when preying on *A. fabae*. This type of response only partially reflects the suitability of *C. undecimpunctata* to control aphid populations, since functional response experiments conducted under laboratory conditions using artificial oversimplified systems cannot give complete information about interactions between predator and prey under natural conditions (Hassell et al., 1977; Ofuya, 1986; Hodek and Honěk, 1996; Munyaneza and Obrycki, 1997; Athhan et al., 2004; Lee and Kang, 2004). Within the field, the area of searching is higher, and plant and field characteristics can also affect the predation response (Hodek and Honěk, 1996; Roger et al,, 2000). Nevertheless, according to Lee and Kang (2004) and Omkar and Pervez (2004), the empirical data on handling time at high aphid density may be comparable with field conditions where the prey density may be high due to heavy aphid infestation.

According to Holling (1959) the number of attacked prey items increases with the total time, prey density and/or attack rate, but decreases as handling time increases. The increase in the number of aphids killed with increasing density may be explained by the fact that at higher prey densities, encounters rates are more frequent and consequently predators consume considerably more than the minimum required (Hodek and Honěk, 1996; Omkar and Pervez, 2004). On other hand, with the increase in prey density, the proportion of partially consumed prey increases, since hungry coccinellids completely devour the first few prey they

Table 2
Attack rate (α) and handling time (T_h) estimated by modified Holling disk equation, and respective standard errors (SE) and 95% confidence intervals, for the 4th instar and adults (females and males) of *C. undecimpunctata* fed on *M. persicae*.

	Parameters	Estimate	Asymptote (SE)	95% CI		
				Lower	Upper	
Larvae (4th instar)	α	0.793	0.044	0.706	0.880	$F_{(2,90)} = 104.4$, $P < 0.05$, $R^2 = 0.93$
	T_h	0.013	0.001	0.011	0.014	
Adult females	α	0.873	0.064	0.746	1.001	$F_{(2,70)} = 78.30$, $P < 0.05$, $R^2 = 0.91$
	T_h	0.015	0.001	0.013	0.017	
Adult males	α	0.923	0.082	0.760	1.087	$F_{(2,70)} = 57.58$, $P < 0.05$, $R^2 = 0.87$
	T_h	0.018	0.001	0.016	0.020	

tackle but gradually extracted smaller proportions of the contents of each aphid killed (Hodek and Honěk, 1996; Omkar and Pervez, 2004). From the perspective of biological control this ability to adjust to variable resources of food could be a very important factor for the effective predator impact on prey (Hodek and Honěk, 1996; Omkar and Pervez, 2004).

A variety of responses had been reported on different coccinellid species, for example, higher handling time (T_h) and attack rate (α) for 4th instar larvae than adults in *H. convergens* (Wells and McPherson, 1999), higher handling time and lower attack rate for 4th instar larvae than adults of *Coleomegilla maculata* DeGeer (Munyaneza and Obrycki, 1997), lower handling time and higher attack rate for 4th instar larvae than adults of *H. axyridis* and *S. creperus* (Lee and Kang, 2004; Wells et al., 2001). In our results, 4th instar larvae displayed a lower handling time (inclusive, significantly lower than adult males) being therefore more efficient on subduing and consuming the prey, and consequently being more voracious than the adults. However, the attack rate was not significantly different between larvae and adults, though it was lower for 4th instar larvae. Moura et al. (2006) had similar results for *C. undecimpunctata* preying on *A. fabae*.

Since ladybird beetles larvae and adults present different dispersion capacities, in this context we foresee that 4th instar larvae will stay longer in the patches, engaged in intensive search activities and thus being very efficient in suppressing prey patches, while the adults will do better in extensive searching and thus will be able to find new aphid patches (Hodek and Honěk, 1996; Kindlmann and Dixon, 2001; Dostalkova et al., 2002) where they can feed and oviposit, given that *M. persicae* is considered an essential prey (i.e., allows both the development and reproduction) to *C. undecimpunctata* (Cabral et al., 2006). We believe that differential searching activities of 4th instar larvae and adults of *C. undecimpunctata* could have synergetic effects on field pest suppression, increasing by this way the success of this species as an agent of biocontrol. From a practical point of view, we suggest that sexually mature adults of *C. undecimpunctata* should be released in the field early in the season, given that it is well established that aphidophagous ladybirds lay mostly their eggs over a relatively short period of time just early before peak aphid infestation (Hemptinne et al., 2000). By having such approach, and according to the foraging theory (Kindlmann and Dixon, 1993; Hemptinne et al., 2000), it is expected that ladybirds will oviposit in the patches that can support the survival of their offspring. Consequently, by the time aphid colonies reach their peaks, there will be many 4th instar larvae of *C. undecimpunctata* within the field engaged in intensive search activities contributing by this way for the suppression of prey patches.

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