



Functional response of four predaceous coccinellids, *Adalia tetraspilota* (Hope), *Coccinella septempunctata* L., *Calvia punctata* (Mulsant) and *Hippodamia variegata* (Goeze) feeding on the green apple aphid, *Aphis pomi* De Geer (Homoptera: Aphididae)

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ABSTRACT: Functional responses of four coccinellids, viz., *Adalia tetraspilota* (Hope), *Coccinella septempunctata* L., *Calvia punctata* (Mulsant) and *Hippodamia variegata* (Goeze), were evaluated under laboratory conditions to find out how these predators responded to density of the prey species, green apple aphid *Aphis pomi* De Geer. All the coccinellid species exhibited a convex (Type II) functional response determined by a non-linear model. The non-linear reciprocal transformation of Hollings, disc equation was used to estimate the parameter values of the model. The large predator, *C. septempunctata* was seen to eat more aphids due to its greater voracity as compared to the smaller species *C. punctata*, *H. variegata* and *A. tetraspilota*. *C. septempunctata* had higher search rate than *C. punctata*, *H. variegata* and *A. tetraspilota*, whereas the handling time showed the opposite trend as the search rate. The results suggest *C. septempunctata* is the best predator for the biocontrol of *Aphis pomi*. Further field-based studies are required to confirm this hypothesis.

KEY WORDS: *Adalia tetraspilota*, *Aphis pomi*, *Calvia punctata*, *Coccinella septempunctata*, functional response, handling time, *Hippodamia variegata*, search rate.

INTRODUCTION

It is well documented that ladybird beetles are very efficient predators of several aphid species (Trouve *et al.*, 1997; Cardoso and Lazzari, 2003). The factors that influence the feeding process and efficiency of these predators as biological control agents are voracity (maximum number of prey consumed by the predator), functional response (the change in the number of prey consumed per predator in response to changing prey density) and

numerical response (the change in predator density resulting from a change in prey density) (Solomon, 1949). Holling (1959, 1965 and 1966) and Trexler *et al.* (1988) reviewed the literature on the functional response of predator to prey density. They classified the functional responses into three main types: an increasing linear relationship (Type I), a curvilinear or a decelerating curve (Type II), or a sigmoidal relationship (Type III). Two other types of functional response have been reported: Type IV (Luck, 1985) and Type V (Sabelis, 1992).

Coccinellids usually show a Type II (curvilinear curve) functional response as reported, for example, for adult female *Adalia bipunctata* (Roche, 1998); *Hippodamia convergens* (Wells and McPherson, 1999); *Coccinella septempunctata* (Ninkovic and Pettersson, 2003); *Propylea dissecta*, *C. transversalis* and *Cheilomenes sexmaculata* (Parvez and Omkar, 2005), *C. septempunctata* and *Chilocorus infernalis* (Khan and Zaki, 2007); and *Eriopis connexa* (Sarmiento *et al.*, 2007).

Type II functional response curves can be characterized by two parameters: the predator's search rate or searching efficiency (a) and its handling time (T_h) (Hassell *et al.*, 1976). The coefficient of searching efficiency determines the steepness of the functional response with increasing prey density, while handling time determines the satiation threshold (Hassell, 1978). *Adalia tetraspilota*, *Coccinella septempunctata*, *Calvia punctata* and *Hippodamia variegata* are aphidophagous ladybird beetles abundant in the horticultural ecosystems of Kashmir, India. Little information is available on the functional responses of these coccinellid species to changes in the densities of *Aphis pomi*. Thus, the present study was designed to investigate the suitability of these coccinellids as biological control agents against *Aphis pomi*, which is an important apple pest in Kashmir.

MATERIALS AND METHODS

Experimental arena and test insects

Laboratory cultures of the four predatory coccinellid species (*Adalia tetraspilota*, *Coccinella septempunctata*, *Calvia punctata*, *Hippodamia variegata*) and the aphid *Aphis pomi* were established from collections during 2007 in an apple orchard belonging to Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Shalimar Campus, Srinagar-191121 (Jammu and Kashmir), India. The coccinellid and aphid cultures were maintained in a culture room at $25 \pm 5^\circ\text{C}$ temperature, $60 \pm 10\%$ relative humidity and a photoperiod of 14 hour light: 10 hour dark.

The adult coccinellids used for the

experiments were taken either from the culture or directly from the field. The adults were placed individually in vials and starved for 24 hrs prior to an experiment in order to minimize differences in individual hunger levels (Nakamura, 1977). Thereafter, they were introduced singly into a separate plastic jar (height 20cm, diameter 15cm) together with 2, 4, 8, 16, 32, 64, 128 or 256 medium size aphids on excised apple leaves stuck to agar medium and covered with a muslin cloth. The test predators were randomly assigned to one of the eight aphid density treatments. One treatment (the control) was also allocated for estimating the natural mortality of aphids. At each aphid density, three replicates were used for each coccinellid species. After 24 hrs, the numbers of aphids consumed by the different predators were recorded by counting the aphids remaining alive in each jar.

Data analysis

Search rates (a) are measured in units of surface area of habitat for a standard cylindrical jar (size 20 cm height and 15 cm diameter) for standard time (cm^2h^{-1}) and handling time (T_h) were in h. The probabilities are generated under the null hypothesis that the fit of equation 3 to data is due to chance.

The number of aphids that have been preyed at the different densities were analyzed for each predator species separately using a non-linear least square programme (R Development Core Team, 2005). Usually, it is difficult distinguish between Type II and III functional responses as mentioned by many workers (Mills, 1982; Trexler *et al.*, 1988). Hence, prior to fitting the data to a particular Holling's Disc equation (1959, 1965) that is Type II functional response:

$$N_a = \frac{a(N/V)T_r}{1 + aT_h(N/V)} \dots\dots\dots(1)$$

where, N_a is the number of prey consumed by one predator during a time period T_r , N is the initial prey density; V is the volume of the experimental cage and a and T_h is as above. However, the above equation describes the instantaneous predation

rates and does not account for the change in prey density during an experiment due to predation (Hassel et al., 1976; Royama, 1971; Rogers, 1972; McArdle and Lawton, 1979). In contrast, the “random predator equation (2)” of Rogers (1972) takes prey exploitation into consideration. It is derived from

$$\frac{dN}{dt} = -\frac{a(N/V)}{1 + aT_h(N/V)} \dots\dots\dots(2)$$

Which integrates to:

$$N_a = \left(\frac{N}{V}\right) \left(1 - \exp(-a(T_i - T_h N_a))\right) \dots\dots\dots(3)$$

Equation 3 now allows *a* and *T_h* to be calculated by iteration from experiments in which the consumed prey individuals are not replaced. In order to avoid the errors incurred by applying the linear regression method to estimate *a* and *T_h* as suggested by Rogers (1972), we used the non-linear function (nls) provided by the R-software (R Development Core Team, 2005).

RESULTS AND DISCUSSION

The functional response of a predator offers an excellent framework for considering the potential action of bioagents in inundative releases (Burgio *et al.*, 2005, Waage and Greathead, 1988). As seen from Fig. 1, the functional responses of *A. tetraspilota*, *C. septempunctata*, *C. punctata* and *H. variegata* to the density of *Aphis pomi* were typically of Type II with a steep initial rise in predation rates as the prey density increased (Table 1). *C. septempunctata*'s consumption increased to 26.06 aphids per day (Fig. 1b) which was higher than that of *C. punctata* (21.73), *H. variegata* (19.73) and *A. tetraspilota* (18.40) (Fig. 1c, Fig. 1d and Fig. 1a). A Type II functional response has been reported for other coccinellid species, e.g. larva of *Harmonia axyridis* (Mogi, 1969), *C. septempunctata* (Sinha *et al.*, 1982, Khan and Zaki, 2007), *A. bipunctata* (Roche, 1998), *Hippodamia convergens* (Cardoso and Lazzari, 2003), *C. transversalis* (Pervez and Omkar, 2005), *C. infernalis* (Khan and Zaki, 2007) and *Eriopis connexa* (Sarmiento *et al.*, 2007).

The larger species, *C. septempunctata* followed by *C. punctata*, were shown to consume more *Aphis pomi* than *H. variegata* and *A.*

Table1. Parameter values of Holling’s disc equation estimated from functional response experiments with predaceous ladybird beetles feeding on green apple aphid, *A. pomi*.

Predatory coccinellids	Parameter	Estimate	SD	t value	r ² at p<0.001	Residual SD
<i>At</i>	<i>a</i>	2.04209	0.29164	7.002	0.6110	0.991
	<i>Th</i>	1.32890	0.06522	20.375		
<i>Cs</i>	<i>a</i>	3.24190	0.58900	5.504	0.6078	1.940
	<i>Th</i>	0.86580	0.05350	16.183		
<i>Cp</i>	<i>a</i>	3.21636	0.53325	5.032	0.5955	1.555
	<i>Th</i>	0.99570	0.05396	18.452		
<i>Hv</i>	<i>a</i>	2.55680	0.27400	9.331	0.5989	0.826
	<i>Th</i>	1.20730	0.04276	28.236		

Adalia tetraspilota =*At*, *Coccinella septempunctata*= *Cs*, *Calvia punctata*= *Cp*, *Hippodamia vareigata*=*Hv*.

tetraspilota. Isikber (2004) reported that the large species *Cycloneda sanguinea* consumed more *Aphis gossypii* than the small species *Scymnus levaillanti*. Similarly, Hemptinne *et al.*, (1996), in an experimental study of two-spotted ladybeetle, *Adalia bipunctata*, on *Acyrtosiphon pisum* found that at high prey densities, females ate more aphids than males to meet growth and reproductive requirements. A comparison of functional response curves revealed that *C. septempunctata* responded more vigorously to lower densities of *A. pomi* than *C. punctata* and *H. variegata* did. However, the number of prey consumed per time unit increases, but the proportion of prey killed declines with prey density if the functional response is Type II. The result indicates that *C. septempunctata* has a higher functional response than any of the three other species at all the densities of prey. Pervez and Omkar (2005) reported that the functional response of *C. transversalis* showed an earlier and steeper increase than that of *Cheilomenes sexmaculata* when the density densities of two aphids, *A. craccivora* and *Myzus persicae* increased and the former species also approached a higher level of predation than the latter.

The results show that a Type II curvilinear curve provides an adequate description of the data. The upper asymptote of the relationship showed indicates the maximum possible predation rate. A non-linear model was further used to detect whether the functional response fitted the data better than a Type III. Such a response could indicate that the predator improved its performance due to switching or learning. Although the logistic model (Juliano, 2001) easily illuminates the delicate differences in Type II and Type III, it fails to distinguish them from a linearly rising curve (Type I). The experimental data, particularly *C. septempunctata* feeding on *A. pomi* at low density, seem to satisfy a Type I functional response; the data were more closely fitted to equation 2. The differences among predator responses at lower and higher prey densities may lead to wrong predictions. Henceforth, efforts must be invested in fitting an analogous logistic model so as to distinguish Type I from II and III (Pervez and Omkar, 2005).

Regrettably, the non-linear model for functional response of predaceous coccinellids is least documented.

The search rate (a) and handling time (Th) estimated for the four coccinellid predators are presented in Table 1 and Figs. 2 and 3 which show that *C. septempunctata* had the highest search rate, followed by *C. punctata*, *H. variegata* and *A. tetraspilota*. The handling times of the predators were just the opposite of the search rates with *A. tetraspilota* being the highest and *C. punctata* the smallest. The effect of different sized coccinellids on the rate of successful encounters with *A. pomi* is shown in Fig.2. Obviously, the search rate is determined by the movement speed, reactive distance at which a predator responds to the prey of presence and prey and the proportion of attacks that are successful (Holling, 1965). The search rate and the handling time are the parameters that reflect the significance of these responses. The fact that these parameters differed significantly among the coccinellid species when exposed to *A. pomi* indicates that the four predator species possess different capacities to pursue prey at increasing aphid densities. It also shows that coccinellids manifesting similar qualitative response curves may not necessarily have the same quantitative impact on the prey. The values of different parameters varied due to the differences in size, greediness, satiation time, hunger levels, digestive power, searching speed, etc. (Ofuya and Akinbohunbe, 1988; Omkar and Pervez, 2004).

Of the four coccinellids, *C. septempunctata* was the one that responded most to increasing densities of *A. pomi*, followed by *C. punctata*, *H. variegata* and *A. tetraspilota*. This result is forcibly supported by empirical data of the reproductive biology of *C. septempunctata*, which acquires greater values in adaptation and reproduction using *A. pomi* than the other species of coccinellids. Handling time differs significantly among predatory coccinellids. The observed handling time is the accumulative impact of time taken during searching and capturing, preying, overpowering and digesting the prey (Omkar and Pervez, 2003). The

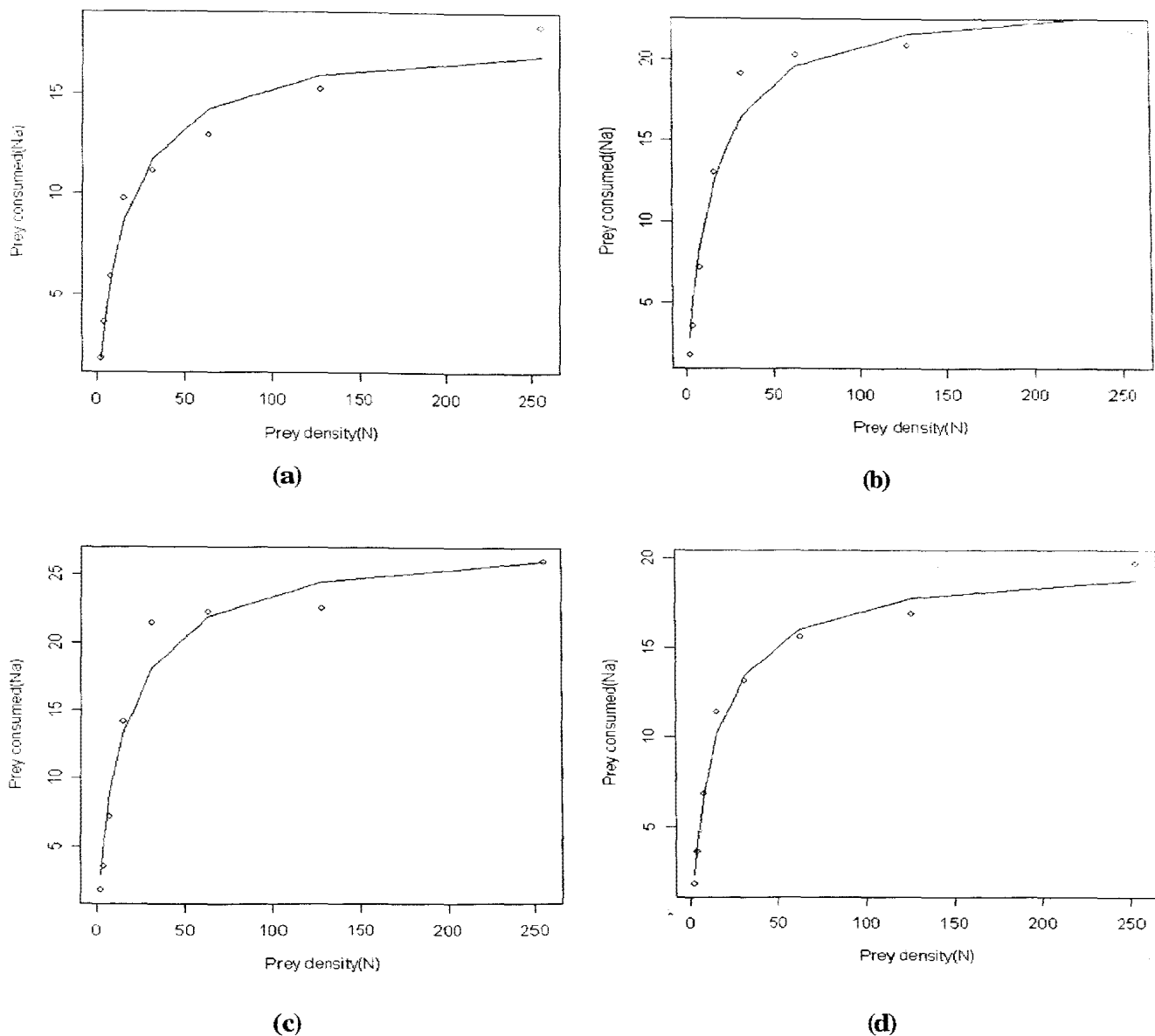


Fig. 1. The mean number of *A. pomi* eaten by individual predaceous ladybird beetles (a) *Adalia tetraspilota* (b) *Coccinella septempunctata* (c) *Calvia punctata* (d) *Hippodamia variegata*. All curves are Type II functional responses fitted by Holling's disc equation model (Holling, 1959) using the parameter values given in Table 1.

significant differences in the estimates of handling times of different predator species on a single prey species indicate that any of these integral components of the handling time might have contributed to the short handling time when *C. septempunctata* was used as a predator rather than *C. punctata*, *H. variegata* and *A. tetraspilota*. This

leads to the presumption that the former species is the one that is most efficient to search, overpower and digest its prey than the other tested coccinellids.

It is concluded that the above-mentioned non-linear model should be included as a decision

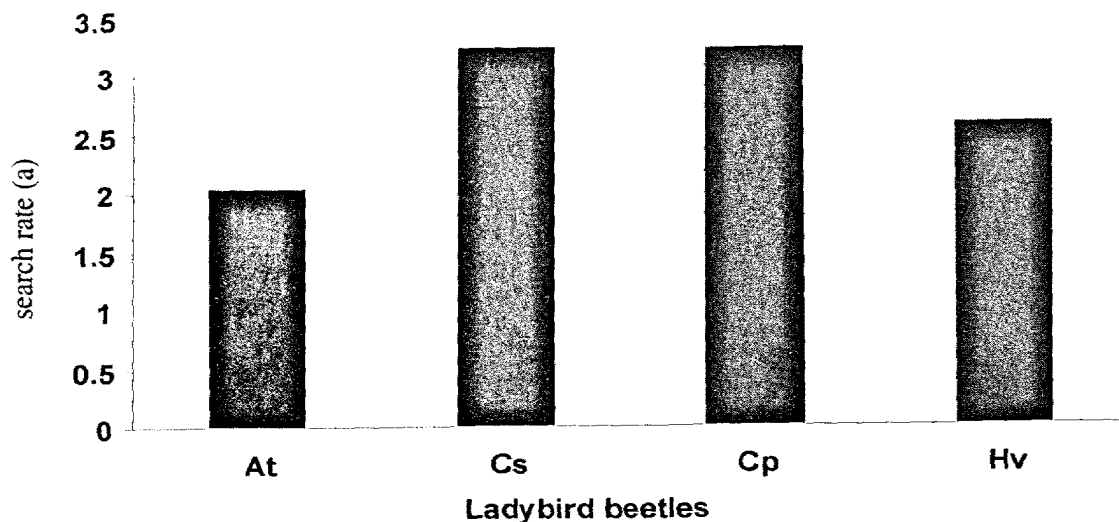


Fig. 2. The search rate (a) for predaceous ladybird beetles preying on *Aphis pomi*. Exact numerical values are given in Table 1.

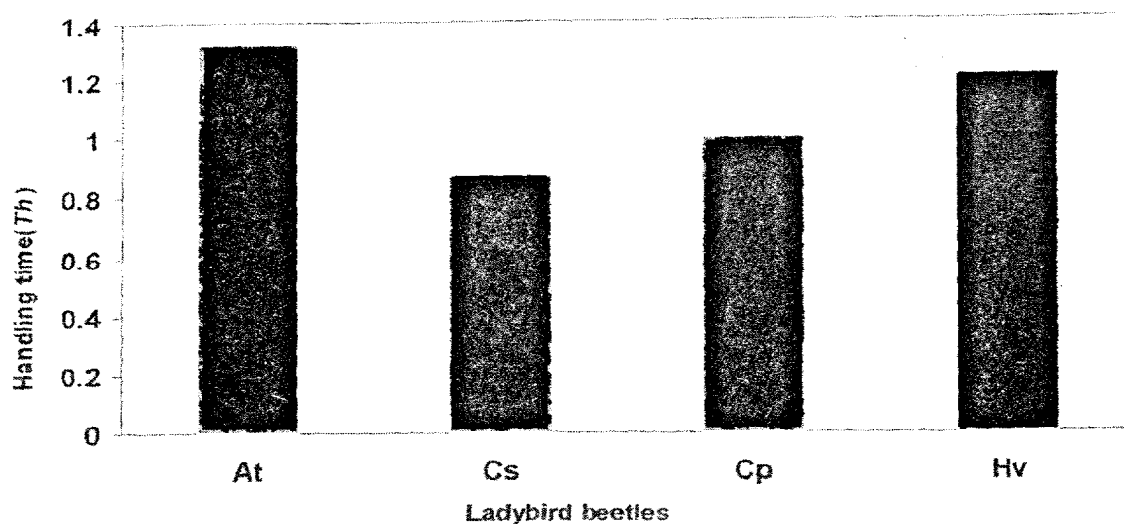


Fig. 3. The handling time (Th) for predaceous ladybird beetles preying on *Aphis pomi*. Exact numerical values are given in Table 1.

tool for investigating the type and shape of functional responses. All the four coccinellids showed Type II functional responses, which varied quantitatively among the species feeding on single *A. pomi*. The highest search rate and lowest handling time was exhibited by *C. septempunctata* followed by *C. punctata*, *H. variegata* and *A. tetraspilota*. *C. septempunctata* has the efficiency to become an important biocontrol agent for the

management of *A. pomi*. However, further field studies are required in order to reveal the predator's capacity under natural conditions.

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