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Functional responses of coccinellid predators: An illustration of a logistic approach

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Abstract

The functional response parameters and patterns of three coccinellid predators, *Cheilomenes sexmaculata*, *Propylea dissecta*, and *Coccinella transversalis* (Coleoptera: Coccinellidae) were evaluated to find out how these predators respond at two different prey species across various prey densities levels. All three predators exhibited a decelerating curve Type II response determined by a logistic regression model. The linear reciprocal transformation of Holling's disc equation was used to further evaluate the parametric values. *C. sexmaculata* responded maximally, followed by *C. transversalis* and *P. dissecta,* in terms of consumption of the aphids, *Aphis craccivora* and *Myzus persicae,* with suitable values of coefficient of attack rates and handling times on these prey species. Differences in handling times were found to be significant within and between the predatory species on both prey species indicating that predators respond differentially to prey species. Differences in coefficients of attack rates, however, did not vary significantly in most of the treatments. The potential role of these predators in biocontrol of *A. craccivora* and *M. persicae* suggests that *C. sexmaculata* is the best predator for the management of both prey species, particularly *A. craccivora*. However, further field based studies are needed to confirm this hypothesis.

Keywords: Aphis craccivora, *Cheilomenes sexmaculata*, *Coccinella transversalis*, Coccinellidae, *Myzus persicae*, *Propylea dissecta*

Introduction

The functional response of a predator is a key factor regulating the population dynamics of predator-prey systems. It describes the rate at which a predator kills its prey at different prey densities and can thus determine the efficiency of a predator in regulating prey populations (Murdoch and Oaten 1975). This is further supported by plotting the number of prey killed against the number of prey available and analyzing a continuum of patterns, which ecologists have delimited into three types (Holling 1959, 1965). The functional response curves may represent an increasing linear relationship (Type I), a decelerating curve (Type II), or a sigmoidal relationship (Type III). This could further be simplified in terms of density dependence. That is, they result in a constant (I), decreasing (II) and increasing (III) rate of prey killing and yield density-dependent, negatively density dependent and positively density dependent prey mortality, respectively. Predators or parasitoids that impose positively density dependence prey mortality (Type III) are supposed to potentially manage the prey population and could be considered as efficient biocontrol agents (Fernández-Arhex and Corley 2003). However, certain predators and parasitoids exhibiting Type II response have been successfully established and managed prey populations (Hughes et al. 1992; Fernández-Arhex and Corley 2003). Usually, a Type III response does not exhibit positive density dependence throughout the range, as only a portion, *i.e.* at the initial level, shows a sigmoidal increase; later on, it also exhibits negative density dependence due to satiation. Hence, it is important to differentiate Type II and III at relatively low prey values. The functional response curves can be differentiated by evaluating the parameters, *viz.* coefficient of attack rate and handling time (time spent by predator in attacking, killing, subduing, and digesting 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.

Ecologists normally face difficulties in determining functional response when the curve lies between Type II and III. Hence, a suitable analysis that can best determine the functional response is highly needed, as it is of great practical relevance in estimating the bio-efficacy of predatory insects (Trexler et al. 1988). Coccinellids are one of the important groups of predatory insects, that have immense biocontrol potential (Omkar and Pervez 2003a) with all three types of functional responses reported for the group (Hodek and Honek 1996). The multi-colored Asian coccinellid, *Harmonia axyridis* is reported to exhibit all three types, i.e. Type I on the aphid, *Rhopalosiphum prunifoliae*) (Lou 1987), Type II on the aphid, *Lipaphis erysim*i (He et al. 1994), and Type III on the aphid, *Cinara* sp. (Hu et al. 1989). Interestingly, on a single prey species, eggs of the monarch butterfly, *Danaus plexippus*, third instars and adults of *H. axyridis* exhibited Type II and Type I responses, respectively (Koch et al. 2003). A single predator can therefore respond differentially to various prey-types and it seems likely that a predator's response to single prey type differs within and between species. An hypothesis was framed that a single predator can exhibit different responses to various prey species.

Cheilomenes sexmaculata (Fabricius), *Coccinella transversalis* Fabricius and *Propylea dissecta* (Mulsant) are

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aphidophagous coccinellids, abundant in the agricultural fields of Lucknow, India. They co-occur in bean (*Dolichos lablab*) and deadly nightshade (*Solanum nigrum*) fields infested with the aphids, *Aphis craccivora* Koch and *Myzus persicae* (Sulzer), respectively. Both *C. sexmaculata* and *C. transversalis* are exhaustively studied coccinellids in the subcontinent as they are highly voracious and fecund, and have a wide prey range, which includes, aphids, coccids, diaspids, aleyrodids, etc. (Agarwala and Yasuda 2000; Omkar and Bind 2004; Omkar and James 2004; Omkar and Pervez 2004a). *P. dissecta,* co-occurring with the above two coccinellid species, is little studied coccinellid. However, recent research has revealed it to be a potential predator of certain aphid species (Pervez and Omkar 2004a). Being ecologically plastic, it can withstand the stresses of prey deprivation and temperature changes (Omkar and Pervez 2003b; Pervez and Omkar 2003; Pervez and Omkar 2004b; Pervez et al. 2004). The present study was thus designed to compare functional responses of the three coccinellids on two aphid species. We also tried to answer the following questions: (i) Are functional responses different among predators when they feed on same prey? (ii) Are the functional responses for each predator different when they feed on different prey? (iii) What is the potential role of these predators for managing *A. craccivora* and *M. persicae* populations?

Materials and Methods

Stock maintenance and experimental design

Adults of *C. sexmaculata*, *C. transversalis*, and *P. dissecta* were collected from *D. lablab* and *S. nigrum* fields infested by *A. craccivora* and *M. persicae*, respectively, and brought to the laboratory. Ten conspecific coccinellids (sex-ratio 1:1) were kept in glass jars (15 × 10 cm) containing moist filter paper for females to oviposit and held at 27 ± 1 °C, 65 ± 5% RH and LD 14:10. The glass jars were covered with muslin and predators fed daily on *ad libitum* food (prey and host as above). The eggs were collected from the filter paper and reared individually from egg hatch to adult eclosion in glass beakers (8 × 11 cm) on the above prey to obtain 10-day-old virgin adult females to be used in experiments.

10-day-old adult females of the three predatory species were kept separately without food for 12 hours in different glass beakers (size as above) in order to standardize their hunger. They were kept separately at different densities, *viz*. 25, 50, 100, 200, 300, and 400 of above prey (each prey species in separate beaker) with host plant twigs in ten replicates (n = 10). The beakers were covered with muslin and kept in an environmental test chamber maintained at 27 °C and 65 ± 5% RH. After 24 hours, the predators removed from the beakers. The number of prey consumed (N_a) were evaluated. Prey were not replaced during the experiment.

Data analysis

Usually, it is difficult to discriminate between Type II and Type III functional responses as mentioned by many workers (Trexler et al. 1988; Casas and Hulliger 1994). Hence, prior to fitting the data to a particular Holling's equation, a logistic regression model (1) was used. This model is used only to determine the shape of functional response by taking into consideration the proportion of prey eaten (N_a/N_o) as a function of prey offered (N_o) (Juliano 2001). The data were fitted to a polynomial function that describes the relationship between N_a / N_o and N_o:

$$\frac{N_a}{N_o} = \frac{\exp(P_o + P_1N_o + P_2N_o^2 + P_3N_o^3)}{1 + \exp(P_o + P_1N_o + P_2N_o^2 + P_3N_o^3)} \quad [1]$$

With P_o, P_1, P_2, and P_3 being the intercept, linear, quadratic and cubic coefficients, respectively, estimated using the method of maximum likelihood. If $P_1 > 0$ and $P_2 < 0$, the proportion of prey consumed is positively density dependent, thus describing a type III functional response. If $P_1 < 0$, the proportion of prey consumed declines monotonically with the initial number of prey offered, thus describing a type II functional response (Juliano 2001). In the above, we used a cubic expression to determine the correctness of the functional response curves because a cubic expression will often provide a good fit to a type III response (Trexler et al. 1988) and will provide a good starting point for fitting a logistic regression (Trexler and Travis 1993). Higher order expression will, of course, fit even better, but this improved fit is usually the result of a better fit to points at higher values of N_o.

After the determination of the shape of the curve, the handling times and attack coefficients of a Type II response were estimated using Holling's disc equation modified by reciprocal linear transformation (Livdahl and Stiven 1983). This method is preferred because of its simplicity (Veeravel and Baskaran 1997; Pervez and Omkar 2003; Omkar and Pervez 2004). The simplified Holling's equation, modified by reciprocal linear transformation (Livdahl and Stiven 1983), is as follows:

$$1 / N_a = 1 / aTN_o + T_h / T \quad [2]$$

where N_a is the number of prey consumed by predator, N_o is the initial prey density, a the attack rate, T the time that predator and prey are exposed to each other, and T_h the handling time associated with each prey consumed. The parameters were obtained by fitting the data to the least square regression.

For a Type III response, model (3) was used as suggested by Hassell et al. (1977), which is as follows:

$$Ne = No \{1-\exp[(d + bNo)(ThNe - T) / (1+ cNo)]\} \quad [3]$$

Where, b, c, and d are constants from the function that relate a and No in type III functional response: a = (d + bNo) / (1 + cNo). Parameters were obtained by fitting observed data to the models above using non-linear least square regression.

To compare type II response of two groups of predators, the following equation was used:

$$Na = No \{1 - \exp[(\hat{a} + \delta a [z]) ([T1h + \delta Th (z)] Na - T)]\} \quad [4]$$

Where z = an indicator variable that takes on the value 0 for predator species one and 1 for predator two. The parameters δ_a and δ_{Th}

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estimate the differences between the individual parameters of a and T_h, respectively of the two coccinellid species. If these parameters are significantly different from 0 then the two predators differ significantly in the corresponding parameters. For predator one, â and $T1_h$ are the estimates of the parameters a_1 and T_{h1}. For predator 2, $\hat{a} + \delta_a$ and $T1_h + \delta_{Th}$, are the estimates of parameters a_2 and T_{h2} (Juliano 2001). The parameters were estimated by non-linear least square regressions. The performance in terms of a and T_h of all three predators tested were compared between and within the species when fed on two prey. This was done by Student t-test followed by Bonferroni's post hoc test of significance using a statistical software MINITAB on personal computer.

Results

The logistic regression for all three predatory species had a significant linear parameter $P_1 < 0$ (Table 1) and the proportion of prey consumed by all predators declined with increasing prey density (Figs 1 and 2). This suggests that all three of them exhibited a Type II response. Their handling times and coefficient of attack rates are presented in Table 2, which shows that *C. transversalis* had the shortest handling time, followed by *C. sexmaculata* and *P. dissecta* using *A. craccivora* as prey. However, when provided with *M. persicae, C. sexmaculata* spent less time in handling the prey, followed by *C. transversalis* and *P. dissecta*. All three predatory species spent relatively more time in handling when *M. persicae* was the prey. Both handling time and coefficient of attack rate were dependent on the prey species with optimal values on *A. craccivora*, followed by *M. persicae* (Table 2).

Comparison of functional response curves revealed that *C. transversalis* responded more vigorously at lower densities of both aphid species with an elevation in the curve over *C. sexmaculata*. However, there was a decline in the consumption rate at higher densities, which resulted in an increase in the functional response curve of *C. sexmaculata*. The functional response curve of *P. dissecta* was significantly lower than the other two predatory species on both prey species (Figs. 1 and 2).

The differences in the attack coefficients and handling times of the three predators on two prey species were compared within and between the species (Tables 3 and 4). Prey species significantly affected the attack coefficients of *C. sexmaculata* and *P. dissecta*, as those obtained on *A. craccivora* were significantly higher than those on *M. persicae*. The differences in the attack coefficients of different predatory species are presented in Table 3, which were largely unaffected by prey species (Table 3), while the handling times mostly showed significant variations both within and between the species (Table 4). This indicates that predators responded differentially in terms of handling time to different prey species.

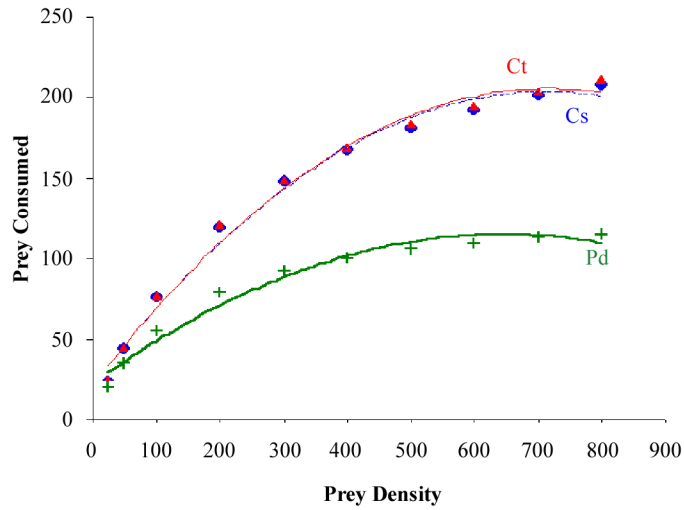

Figure 1. Type II Functional response of ladybirds, *C. sexmaculata (Cs) C. transversalis (Ct),* and *P. dissecta (Pd)* at different densities of *A. craccivora* (derived using Livdahl & Stiven Model (N=1)).

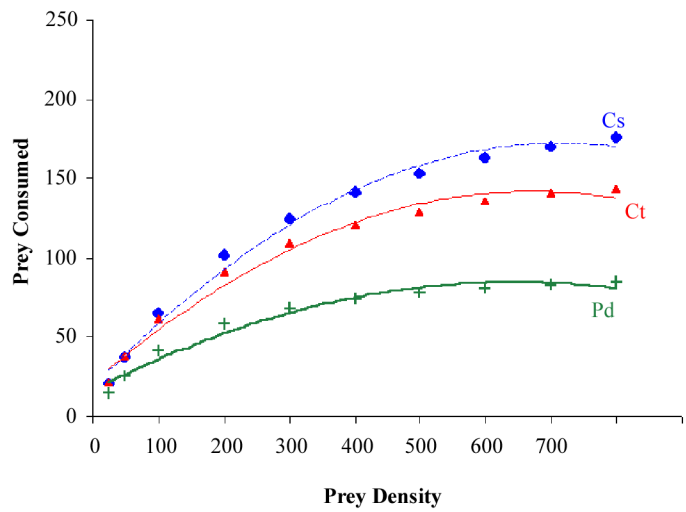

Figure 2. Type II Functional response of ladybirds, *C. sexmaculata (Cs) C. transversalis (Ct)*, and *P. dissecta (Pd)* at different densities of *M. persicae* (derived using Livdahl & Stiven Model (N=1)).

Discussion

The results revealed that a Type II asymptotic curve described the data well. The asymptote in the curve reveals the point of maximum consumption rate. A logistic regression model was further used to determine the correctness of the shapes, as in such studies ecologists normally face difficulties in curve-fitting when the data set of Type II response shows inclination towards Type III response. This can lead to drawing misleading inferences (as one shows negative density dependence while other shows positive density dependence), which further might lead to erroneous predictions about the fate of prey-predator interactions. The negative values for the linear parameters ($P_1 < 0$) obtained in the present study confirm the Type II response for all three predators used. The logistic regression model thus can be recommended as a tool for further analyzing functional response curves.

A Type III functional response shows a positive density dependence of the proportion of prey killed as the density increases, hence a polynomial fit to a Type III should have a linear term that is positive. Conversely, for a Type II response, there should be a decline

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Table 1. Maximum likelihood estimates from logistic regression of proportion of prey eaten as a function of initial prey densities by adult females of C. sexmaculata, C. transversalis and P. dissecta (n=10).

		A. craccivora				*M. persicae*			
Ladybird species	**Parameters**	**Estimate**	**SD**	**t- ratio**	**P**	**Estimate**	**SD**	**t-ratio**	**P**
	Intercept (P_o)	1.08322	0.02255	48.03	0.000	0.94019	0.02813	33.43	0.000
	Linear (P_1)	-0.0053127	0.0005457	-9.74	0.000	-0.0047608	0.0006808	-6.99	0.000
C. sexmaculata	Quadratic (P_2)	0.0000185	0.00000306	6.04	0.000	0.00001582	0.00000382	4.14	0.000
	Intercept (P_o)	1.01633	0.03139	32.38	0.000	0.7143	0.02685	26.6	0.000
	Linear (P_1)	-0.0072528	0.0007595	-9.55	0.000	-0.046829	0.0006498	-7.21	0.000
P. dissecta	Quadratic (P_2)	0.00002719	0.00000426	9.68	0.000	0.0000165	0.0000036	4.53	0.000
	Intercept (P_o)	1.10523	0.03491	31.66	0.000	0.9746	0.03946	24.7	0.000
	Linear (P_1)	-0.0066067	0.0009832	-9.55	0.000	-0.006305	0.000111	-5.67	0.000
C. transversalis	Quadratic (P_2)	0.00002496	0.00000632	4.66	0.000	0.00002775	0.00000715	3.88	0.000

Table 2. Coefficient of attack rate (a) and handling time (T_h) of *C. sexmaculata, P. dissecta* and *C. transversalis* derived from Livdahl and Stiven Model using A. craccivora and M. persicae as prey (T=1day).

Ladybird species	**Aphid Species**	**a**	**Th (in min)**		**r2 at P<0.001**
	A. craccivora	1.06	5.24	(0.0036)*	0.98
C. sexmaculata	*M. persicae*	0.9	6.2	(0.0043)*	0.96
	A. craccivora	0.94	10.6	(0.0074)*	0.93
P. dissecta	*M. persicae*	0.7	14.4	(0.01)*	0.94
	A. craccivora	1.05	5.15	(0.0036)*	0.97
C. transversalis	*M. persicae*	0.94	8.11	(0.0056)*	0.96

Table 3. D_a values when comparing coefficient of attack rates of three predatory species on two aphid prey, *A. craccivora* and *M. persicae* both between and within the predatory species.

	A. craccivora			*M. persicae*			*A. craccivora*
Ladybird species	***Cs***	***Pd***	***Ct***	***Cs***	***Pd***	***Ct***	***M. persicae***
C. sexmaculata	-	0.12 (NS)	0.01 (NS)	-	0. 02 (NS)	-0.04 (NS)	0.16 (P<0.01)
P. dissecta	-0.12 (NS)	-	-0.11 (NS)	-0.20 (P<0.01)	-	-0.24 (P<0.01)	0.24 (P<0.01)
C. transversalis	-0.01 (NS)	0.11 (NS)	-	0.04 (NS)	0.24 (P<0.01)	-	0.11 (NS)

Table 4. D_{Th} values when comparing handling times of three predatory species on two aphid prey, *A. craccivora* and *M. persicae* both between and within the predatory species.

	A. craccivora			*M. persicae*			*A. craccivora*
Species	***Cs***	***Pd***	***Ct***	***Cs***	***Pd***	***Ct***	***M. persicae***
C. sexmaculata	-	-5.35 (P<0.001)	0.09 (NS)	-	-8.20 (P<0.001)	-1.91 (P<0.01)	-0.96 (P<0.05)
P. dissecta	5.35 (P<0.001)	-	5.45 (P<0.001)	8.20 (P<0.001)	-	6.29 (P<0.001)	-3.8 (P<0.001)
C. transversalis	-0.09 (NS)	-5.45 (P<0.001)	-	1.91 (P<0.01)	-6.29 (P<0.001)	-	-2.96 (P<0.001)

in the proportion killed as the density increases, so that the linear term should be negative. However, very rarely, it is possible to get a Type II response with a positive linear term, if negative quadratic or cubic terms are sufficiently large (Juliano personal communication). Although the logistic model (Juliano 2001) easily illuminates the subtle differences in the Type II and III responses, it fails to discriminate them from Type I (linear). The empirical data, especially *C. sexmaculata* preying on *A. craccivora* at lower prey densities, appears to support a Type I functional response. However, the Type I equation (Holling 1959) does not give the best fit to the data. The data were

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more closely fitted to equation 2. The differential response of predator at lower and higher prey densities might lead to erroneous predictions. Hence, efforts are needed to make a similar logistic model to differentiate Type I from II and III. Unfortunately, the linear functional response in predatory coccinellids is least reported. The functional response parameters obtained by reciprocal transformation (Livdahl and Stiven 1983) gave the best fit to the data, and can be used to determine the simulated N_a value at any prey density. Thus, minimizing the efforts needed to generate voluminous empirical data at different aphid densities in the laboratory.

The coefficient of attack rate and handling time were the parameters used to find out the magnitude of these responses. Their values differed significantly within and between the predatory species when exposed to two prey species, which indicate that they have different abilities to respond to increasing prey densities. This also indicates that predators exhibiting similar functional response curves cannot be deemed to respond similarly. The differences in parametric values might be due to the variation in size, voracity, satiation time, hunger levels, digestive ability, walking speed, etc. (Mills 1982; Ofuya and Akinbohungbe 1988; Omkar and Pervez 2004b).

Amongst the three predators, *C. sexmaculata* responded maximally to increasing densities of *A. craccivora*, followed by *C. sexmaculata* and *P. dissecta*. This inference is strongly supported by the empirical evidence of the reproductive biology of *C. sexmaculata*, which obtains higher values in fitness and reproduction using this prey species (Omkar and Bind 2004). As is evident from the functional response curve, the relative rate of prey consumption by *C. transversalis* was higher at lower densities on both prey species, indicating that it could be more effective at lower prey densities. It exhibited a significant decline in consumption rate at higher prey densities, which might be due to the attainment of satiation (Mills 1982). The elevated functional response curve that *C. sexmaculata* attained over that of *C. transversalis* indicates a possible delayed satiation and/or a possible faster digestive rate. A high rate of prey consumption at higher densities is not a feature of aphidophagous coccinellid predators (Pervez and Omkar 2003b), which is a major reason for the failure in aphid biocontrol programs using predatory coccinellids.

The differences in the coefficients of attack rates did not vary significantly in most of the treatments, which indicates that this parameter is least affected by the change in predator and/or prey species. Similar insignificant effects of predator and prey types were reported in four heteropteran predators preying on whiteflies and thrips (Montserrat et al. 2000). The differences in handling times varied significantly both within and between the predatory species. The handling time estimate is the cumulative effect of time taken during capturing, killing, subduing, and digesting the prey (Veeravel and Baskaran 1997). Thus, significant variation in the estimates of handling times of a single predator on different prey species indicates that any one of these integral components of the handling time might have been negatively affected when *M. persicae* was used as prey rather than *A. craccivora*. This leads to the inference that though these predators co-occur in *M. persicae* colonies, they will be more efficient if employed against *A. craccivora* infestations.

Functional response, though an important tool, cannot only be attributed to reported success and failures in biocontrol programs. For instance, other factors, such as intrinsic growth rates, host patchiness, predation and competition, host traits, and environmental complexities (abiotic and biotic factors) also have a major influence on the efficiency of predator in managing the prey population. Our laboratory data provide information as to how these predators will respond to increasing prey density under simplified experimental conditions. For conclusive estimations of their biocontrol potential, further field based studies are needed. However, from the evidence of functional response curves, coefficient of attack rates and handling time, we can predict that among the three co-occurring predatory species, *C. sexmaculata* could be an efficient biocontrol agent, supporting our first hypothesis that predators respond differentially. The differential functional response of predators on *A. craccivora* and *M. persicae* obtaining higher parametric values using former prey supports our second hypothesis that predators respond differentially to various prey species.

It can be concluded that the preceding logistic regression model should be encouraged for the conclusive analysis of functional responses. All three predators exhibited Type II response, which varied differentially within and between the species on two aphid species used. Maximal values for coefficient of attack rate and handling time were obtained by *C. sexmaculata*, followed by *C. transversalis* and *P. dissecta*. All three predators were more effective against *A. craccivora* rather than *M. persicae*. *C. sexmaculata* has the potential to be exploited successfully as a biocontrol agent for the management of *A. craccivora* infestations; however, further field-based studies are needed.

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