The Canadian Entomologist (2022), **154**, e11, 1–14
doi:10.4039/tce.2021.59

Published on behalf of the Entomological Society of Canada

ARTICLE

Functional response in coccinellid beetles (Coleoptera: Coccinellidae) is modified by prey-density experience

Desh Deepak Chaudhary[1], Bhupendra Kumar[2], Geetanjali Mishra[3], and Omkar[3]*

[1]Department of Zoology, Indira Gandhi National Tribal University, Amarkantak, Madhya Pradesh, 484887, India, [2]Department of Zoology, Banaras Hindu University, Varanasi, Uttar Pradesh, 221005, India, and [3]Ladybird Research Laboratory Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh, 226007, India
*Corresponding author. Email: omkar.lkouniv@gmail.com

(Received 15 May 2021; accepted 8 September 2021)

Abstract

In the present study, we assessed functional response curves of two generalist coccinellid beetles (Coleoptera: Coccinellidae), specifically *Menochilus sexmaculatus* and *Propylea dissecta*, using fluctuating densities of aphid prey as a stimulus. In what may be the first such study, we investigated how the prey density experienced during the early larval development of these two predatory beetle species shaped the functional response curves of the late instar–larval and adult stages. The predators were switched from their rearing prey-density environments of scarce, optimal, or abundant prey to five testing density environments of extremely scarce, scarce, suboptimal, optimal, or abundant prey. The individuals of *M. sexmaculatus* that were reared on either scarce- and optimal- or abundant-prey densities exhibited type II functional response curves as both larvae and adults. However, individuals of *P. dissecta* that were reared on scarce- and abundant-prey densities displayed modified type II functional response curves as larvae and type II functional response curves as adults. In contrast, individuals of *P. dissecta* reared on the optimal-prey density displayed type II functional response curves as larvae and modified type II functional response curves as adults. The fourth-instar larvae and adult females of *M. sexmaculatus* and *P. dissecta* also exhibited highest prey consumption (T/T_h) and shortest prey-handling time (T_h) on the scarce-prey rearing density. Thus, under fluctuating-prey conditions, *M. sexmaculatus* is a better biological control agent of aphids than *P. dissecta* is.

Introduction

Insects respond to diverse external cues when they search for food, shelter, mates, and oviposition locations (Dukas 2008). Responses to most of these cues are innate, although some might be learned (Remén 2004; Giurfa 2013, 2015). Learning helps insects to adapt to their current environment (Moreyra and Lozada 2021). However, the speed, reversibility, and mechanism of learning are related to the frequency with which insects must switch resources in their lifetime (Vet and Dicke 1992). The ability to learn differs among insect taxa, and some predatory groups are more prepared to learn certain stimuli than others are (Papaj and Lewis 2012). The rates at which insect predators encounter prey likely increase if the learned information facilitates their prey-searching process (Papaj and Lewis 2012). However, because the process of learning takes time, learning might have negative effects if the environment changes too quickly (Remén 2004).

A changing environment acts directly upon the environment-sensitive physiological processes of insect predators (Bell 1990). The predators perceive such changes in the environment and,

Subject editor: Christie Bahlai

© The Author(s), 2022. Published by Cambridge University Press on behalf of the Entomological Society of Canada

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

based on that information, might alter their behaviour (Bell 1990). Studies have shown that under changing environmental conditions, the availability of prey often fluctuates (Dixon 2000; Hodek *et al.* 2012). This, in turn, influences the vital rates and population dynamics of predators (Ostfeld and Keesing 2000).

Coccinellids (Coleoptera: Coccinellidae) are an important group of insect predators, and they are the most successful biocontrol agents of aphids and other insect and acarine pests (Hodek and Honek 1996; Hodek *et al.* 2012). However, their ability to learn has not been studied extensively (Remén 2004). Few studies have looked into coccinellid learning (Mondor and Warren 2000; Ninkovic and Pettersson 2003), and the studies that have been undertaken have all suggested that visual and olfactory cues drive coccinellids' detection of their prey. Aphidophagous coccinellid beetles are best at exploiting aphids, whose populations fluctuate rapidly in space and time, thereby severely affecting the life attributes of coccinellids (Santos-Cividanes *et al.* 2011). The most informative way to study the response of coccinellid beetles to aphid fluctuations is to measure the beetles' functional responses to different aphid abundances (Fathipour *et al.* 2006; Bayoumy 2011a, 2011b; Bayoumy and Michaud 2012).

Several studies have evaluated the functional responses of coccinellids, both individually (Bayoumy 2011a; Osman and Bayoumy 2011; Gupta *et al.* 2012) and within guilds (Snyder and Ives 2003; Snyder 2009; Grez *et al.* 2011, 2012; Omkar and Pervez 2011; Jamour and Shishehbor 2012; Vanaclocha *et al.* 2013; Kumar *et al.* 2014a), and report either a type II or a modified type II functional response. Despite the important role of predation in shaping community structure, comparisons of functional responses of coccinellids under fluctuating-prey conditions are rarely investigated (Hiltunen and Laakso 2013). In addition, the role of learning in modulating the functional response curves of coccinellid beetles has rarely been studied.

In the present study, we investigated the functional responses of two coccinellid beetles, *Menochilus sexmaculatus* and *Propylea dissecta*, under varying aphid abundances to assess whether the prey density experienced during early larval development would affect the functional response curves of the beetles' late-larval and adult stages. We hypothesised that, under rearing conditions, the larvae and adults would learn to use the available prey resource with their usual predation rates but that, when tested under different prey-density conditions, the larvae and adults would modulate their predation attributes in response to the available prey resource. We hypothesised that, as a consequence of this, the beetles reared on scarce prey would exhibit higher functional response curves than those reared on optimal- or abundant-prey densities when the beetles suddenly encountered prey-resource fluctuations or irregular prey densities.

The two beetle species investigated in the present study are Asian predatory coccinellids, have wide prey ranges, and coexist abundantly in aphid-infested agricultural fields of India (Omkar and Pervez 2000). The present study provides information on the feeding behaviour of these beetles in relation to varying prey density and also contributes to the understanding of the biological control potential of these beetles under fluctuating resource conditions.

Materials and methods

Stock maintenance

Adult males and females of *M. sexmaculatus* and *P. dissecta* were collected from agricultural fields in Lucknow, India (26° 50′ N, 80° 54′ E) and paired randomly in plastic Petri dishes ($9.0 \times 1.5\ cm^2$). The insects were reared under 27 ± 2°C temperature, 65 ± 5% relative humidity, and a 14:10 light:dark photoperiod in environmental test chambers (York BOD incubator, Super Deluxe, Yorco Scientific Industries Pvt. Limited, Ghaziabad, Uttar Pradesh, India) on daily replenished supply of cowpea aphid, *Aphis craccivora* Koch (Hemiptera:

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Aphididae) that had been reared on bean (*Dolichos lablab* Linnaeus) (Fabaceae) in a polyhouse (Chaudhary *et al.* 2016). Beetle eggs laid were collected every 24 hours, and the subsequent first-instar larvae were used for further experimentation.

Experimental design

Our study comprised three experiments. The first experiment optimised different food conditions for life stages of both coccinellid species. The second experiment investigated the rearing of beetle larvae under scarce-, optimal-, and abundant-prey conditions (herein referred to as "rearing prey densities") until the emergence of fourth-instar larvae and adults. The third experiment evaluated the functional response of fourth-instar beetle larvae and 10-day-old unmated females under five prey densities – extremely scarce, scarce, suboptimal, optimal, and abundant (herein referred to as "testing prey densities").

The fourth-instar larvae and 10-day-old unmated females are the most voracious feeding stages of coccinellids that are generally employed in biological control programmes (Mishra *et al.* 2012; Omkar *et al.* 2014). Because of this, the functional response experiments were conducted with only these two developmental stages.

Prey optimisation

Individual fourth-instar larvae of both coccinellid species were provided with aphid biomass ranging from 1 to 20 mg (*i.e.,* 1, 2, 5, 10, 15, and 20 mg) of intermediate instars (*i.e.,* second and third nymphal stages) of *A. craccivora* for 24 hours in five replicates. Biomass was measured using the Sartorius Weighing Balance BSA 124 S-CW (0.01 mg precision; Sartorius Lab Instruments GmbH & Co. KG, Goettingen, Germany). The minimum biomass at which no aphid was left and the larvae survived was considered the "scarce" prey-density condition, whereas the minimum biomass at which aphids were left (1.00 ± 0.50 mg) in some replicates and larvae survived was referred to as the "optimal" prey-density condition. The replicates in which a minimum biomass of 4.00 ± 1.00 mg was left were referred to as the "abundant" prey-density condition. Based on the optimisation experiment, the scarce, optimal, and abundant prey biomasses were 2, 10, and 15 mg of aphids per individual beetle per day, respectively. However, the "extremely scarce" and "suboptimal" prey biomasses were found to be 1 and 5 mg of aphids per individual beetle per day, respectively (see Chaudhary *et al.* 2015).

Exposure of predatory stages to three rearing prey densities

The first-instar larvae of *M. sexmaculatus* and *P. dissecta* were individually reared under scarce ($n = 150$ larvae per coccinellid species), optimal ($n = 150$ larvae per coccinellid species), and abundant ($n = 150$ larvae per coccinellid species) prey densities up to the third-instar larval stage under abiotic conditions similar to that of stock culture. After the third-instar larvae moulted to the fourth-instar stage, 10 larvae per coccinellid species from each rearing prey density were used to assess their functional response on each testing prey density. After completion of the experiment, the fourth-instar larvae per rearing density were shifted to their respective prey biomass until they became 10-day-old adults. Thereafter, 10 adult females from each rearing prey density were identified, separated, and used in the experiment to assess their functional response on each testing prey density.

A total of 20 larvae of *M. sexmaculatus* and 30 larvae of *P. dissecta* died before reaching the fourth-instar stage when fed under the scarce-prey conditions. After that, more first-instar larvae of each coccinellid species from the stock cultures were added to the experimental setup to equalise the sample size to 50 individuals at each of the three prey densities.

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Functional responses of predatory stages under five testing prey densities

The fourth-instar larvae ($n = 50$ larvae per coccinellid species) from each rearing prey density were divided into five groups of 10 each. The beetles (*M. sexmaculatus* or *P. dissecta*) were kept singly in Petri dishes (size mentioned above) in the above-described abiotic conditions for 24 hours and provided with prey comprising second- and third-instar larvae of *A. craccivora* in the following amounts: (1) extremely scarce supply (1 mg); (2) scarce supply (2 mg); (3) suboptimal supply (5 mg); (4) optimal supply (10 mg), or (5) abundant supply (15 mg). After 24 hours, the prey remaining were weighed in their respective Petri dishes separately from the beetles.

The same experiment was replicated with 10-day-old unmated adult female beetles from each prey supply. The adult females were divided into five groups of 10 each, giving a total of 50 females per coccinellid species, and shifted to extremely scarce, scarce, suboptimal, optimal, or abundant prey conditions under the above abiotic conditions. The rest of the experimental protocol described above was applied.

The natural reduction in aphid biomass in the absence of predators, if any, was analysed by keeping 1, 2, 5, 10, and 15 mg of preweighed aphids, in five replicates each, under similar abiotic conditions for 24 hours and then reweighed, with the average loss in aphid biomass thereby determined. Using the average loss in aphid biomass in the absence of predators, the loss in biomass of aphid prey left remaining by the individual predator (larva or adult) after 24 hours was determined. Then the loss in biomass of aphid prey left remaining by individual predator after 24 hours was deducted from the aphid biomass consumed by that predator in 24 hours to determine the predator's actual consumption rate.

Statistical analysis

The distribution of data sets obtained in the present study was checked for normality using the Kolmogorov–Smirnoff test. The means were separated using Tukey's test when data were normally distributed, and the variances were found to be homogeneous (Bartlett's test for equal variances).

Analyses of the functional responses recorded involved determining the type of functional response and estimating the parameters of functional response curves (Juliano 2001). Initially, to discriminate type II and type III responses, the shape of functional response curve was analysed using a logistic regression (Juliano 2001) of the proportion of prey consumed (N_e) as a function of initial prey biomass provided (N_o). The data were fitted to a polynomial regression function. The equation used was:

$$\frac{N_e}{N_o} = \frac{\exp\left(P_o + P_1N_o + P_2{N_o}^2 + P_3{N_o}^3\right)}{1 + \exp\left(P_o + P_1N_o + P_2{N_o}^2 + P_3{N_o}^3\right)} \quad (1)$$

where P_o (intercept), P_1 (linear), P_2 (quadratic), and P_3 (cubic) were the parameters to be estimated. Positive linear ($P_1 > 0$) and negative quadratic ($P_2 < 0$) parameters indicate a type III functional response. If P_1 is less than zero, the proportion of prey biomass consumed declines monotonically with the initial biomass of prey offered, suggesting a type II functional response (Juliano 2001). The Proc CATMOD procedure (Juliano 2001) was used to estimate these parameters. The second analysis used a nonlinear least-squares regression, Proc NLIN (Juliano 2001), to estimate the parameter values (T_h and either a for type II or b, c, and d for type III). Because the experiment was carried out without replacing prey biomass that were eaten, the appropriate model for a Type II functional response is the "random-predator" equation (Roger 1972):

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

$$N_e = N_o\{1 - \exp[a(T_h N_e - T)]\} \text{ type II} \quad (2)$$

For modelling the type III response, the attack rate (a) in equation 3 was set in equation 2 as a function of prey density (Hassell 1978). In the simplest generalised form, attack rate (equation 3) is a function of the initial biomass of prey:

$$a = \frac{d + b\,N_o}{1 + c\,N_o} \quad (3)$$

in which b, c, and d are constants that must be estimated. The simplest form arises when a is a function of initial density, as in equation 4.

$$N_e = N_o\{1 - \exp[(d + bN_o)(T_h N_e - T)/(1 + cN_o)]\} \text{ type III} \quad (4)$$

where N_e is the number of prey consumed, N_o is the initial prey biomass, T_h is the handling time per prey, T is the total time of exposure, and b, c, and d are constants. The parameters T_h and a in this case were also obtained using equation 2. All statistical analyses were performed using SAS, version 9.0 (SAS Institute Inc., Cary, North Carolina, United States of America; https://www.sas.com (accessed 14 October 2020)).

Results

In the present study, the decreased proportion of prey consumed by the predatory stages when provided with an increased biomass of aphid prey points to a type II functional response. From the results of our maximum-likelihood analyses, type II functional response is confirmed for *M. sexmaculatus* fourth-instar larvae and adult females under the scarce, optimal, and abundant rearing prey densities, and for *P. dissecta* fourth-instar larvae under the optimal rearing prey density and *P. dissecta* adult females under the scarce and abundant rearing prey densities (Tables 1 and 2). By plotting a type II functional response and then fitting polynomial logistic regression models to the biomass and proportions of prey consumed, respectively, the resulting regression lines fitted the data well (Figs. 1, 2, 3, and 4).

However, significant positive linear and negative quadratic coefficients for *P. dissecta* fourth-instar larvae under the scarce and abundant rearing prey densities and for this species' adult females under the optimal-prey rearing density suggested a type III functional response (Tables 1 and 2). For this reason, equation 3 was substituted in equation 2, and the two data sets were fit to a type III functional response curve. Results of the nonlinear least-squares regression indicated that parameters c and d did not significantly differ from zero; therefore, they were removed from the model, and a reduced model (equation 4) was used (Juliano 2001). Furthermore, the proportion of prey consumed (N_e/N_0) by *P. dissecta* fourth-instar larvae under the scarce and abundant rearing prey densities and this species' adult females under the optimal-prey rearing density did not increase with increased prey density as usually observed for a type III functional response; instead, it decreased when the biomass of prey provided was increased, similar to a type II functional response. This would therefore suggest a modified type II functional response for these predators (Figs. 1, 2, 3, and 4; see Chaudhary *et al.* 2015; Patel *et al.* 2017).

The results also revealed that the attack rate (a) was highest for *M. sexmaculatus* and *P. dissecta* fourth-instar larvae under the optimal rearing prey density, whereas the adult females of the two predators demonstrated the highest attack rate under the abundant and scarce rearing prey densities, respectively. However, both species' fourth-instar larvae and adult females showed the shortest prey-handling time (T_h) under the scarce rearing prey density. Moreover, the consumption of prey over 24 hours (T/T_h) was greatest when both species' fourth-instar larvae and adult females were reared under the scarce-prey density (Table 3).

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Table 1. Functional response parameters exhibited by fourth-instar larvae of *Menochilus sexmaculatus* and *Propylea dissecta* when fed on different densities of prey.

Predator species	Rearing conditions	Parameters	Estimates	Standard error	χ^2-value	*P*-value
M. sexmaculatus	**Scarce	Intercept (P_o)	3.615	2.329	2.41	0.121
		Linear (P_1)	–0.043	1.103	0.00	0.969
		Quadratic (P_2)	–0.009	0.141	0.00	0.947
		Cubic (P_3)	0.000	0.005	0.00	0.997
	**Optimal	Intercept (P_o)	3.935	2.360	2.78	0.096
		Linear (P_1)	–0.345	1.124	0.09	0.759
		Quadratic (P_2)	0.054	0.145	0.14	0.710
		Cubic (P_3)	–0.003	0.05	0.32	0.570
	**Abundant	Intercept (P_o)	4.520	2.301	3.86	0.050
		Linear (P_1)	–0.728	0.977	0.55	0.457
		Quadratic (P_2)	0.061	0.119	0.32	0.571
		Cubic (P_3)	–0.002	0.004	0.33	0.564
P. dissecta	*Scarce	Intercept (P_o)	3.046	2.335	1.70	0.192
		Linear (P_1)	0.449	1.167	0.15	0.700
		Quadratic (P_2)	–0.087	0.152	0.33	0.568
		Cubic (P_3)	0.003	0.006	0.33	0.568
	**Optimal	Intercept (P_o)	5.174	2.368	4.77	0.029
		Linear (P_1)	–1.332	1.036	1.66	0.198
		Quadratic (P_2)	0.200	0.131	2.34	0.126
		Cubic (P_3)	–0.009	0.005	3.27	0.071
	*Abundant	Intercept (P_o)	2.508	2.283	1.21	0.272
		Linear (P_1)	0.984	1.137	0.75	0.387
		Quadratic (P_2)	–0.199	0.147	1.83	0.176
		Cubic (P_3)	0.008	0.005	2.34	0.126

*A positive estimate for parameter P_1 and significant negative estimate for P_2 indicate a type III functional response. **A significant negative estimate for parameter P_1 indicates that the slope of the functional response curve is declining, which indicates a type II functional response.

The beetles of both the species had lower prey-handling time and higher prey consumption as adults than as larvae. However, between the two coccinellid species, *M. sexmaculatus* consumed more prey than *P. dissecta* did.

Discussion

In the present study, negative linear coefficients (P_1) for *M. sexmaculatus* fourth-instar larvae and adult females that had been reared on the scarce, optimal, and abundant prey densities but were provided with the five testing prey densities revealed that the rate of prey consumption decreased with increase in abundance of prey, which functionally indicates a type II response. Similar type II–response results were obtained both for *P. dissecta* fourth-instar larvae that had been reared under the optimal rearing prey density and then were provided with the five testing prey densities and for the species' adult females that had been reared under scarce and

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Table 2. Functional response parameters exhibited by adult females of *Menochilus sexmaculatus* and *Propylea dissecta* when fed on different densities of prey.

Predator species	Rearing conditions	Parameters	Estimates	Standard error	χ^2-value	*P*-value
M. sexmaculatus	**Scarce	Intercept (P_o)	4.748	2.303	4.19	0.041
		Linear (P_1)	−0.937	0.991	0.89	0.345
		Quadratic (P_2)	0.112	0.122	0.84	0.359
		Cubic (P_3)	−0.004	0.004	0.98	0.321
	**Optimal	Intercept (P_o)	4.599	2.294	4.02	0.045
		Linear (P_1)	−0.765	0.958	0.64	0.425
		Quadratic (P_2)	0.060	0.115	0.28	0.599
		Cubic (P_3)	−0.001	0.004	0.19	0.662
	**Abundant	Intercept (P_o)	4.464	2.326	3.68	0.055
		Linear (P_1)	−0.728	1.023	0.51	0.476
		Quadratic (P_2)	0.089	0.127	0.48	0.487
		Cubic (P_3)	−0.003	0.005	0.65	0.421
P. dissecta	**Scarce	Intercept (P_o)	5.582	2.390	5.46	0.020
		Linear (P_1)	−1.659	1.040	2.54	0.111
		Quadratic (P_2)	0.254	0.133	3.66	0.056
		Cubic (P_3)	−0.011	0.005	4.84	0.028
	*Optimal	Intercept (P_o)	0.126	3.019	0.00	0.967
		Linear (P_1)	3.236	2.480	1.70	0.192
		Quadratic (P_2)	−0.506	0.356	2.01	0.156
		Cubic (P_3)	0.020	0.014	2.06	0.152
	**Abundant	Intercept (P_o)	3.770	1.012	13.86	0.0002
		Linear (P_1)	−0.109	0.145	0.57	0.450
		Quadratic (P_2)	−0.034	0.176	2.23	0.136
		Cubic (P_3)	0.002	0.000	21.47	<0.0001

*A positive estimate for parameter P_1 and significant negative estimate for P_2 indicate a type III functional response. **A significant negative estimate for parameter P_1 indicates that the slope of the functional response curve is declining, which indicates a type II functional response.

abundant prey densities and then were provided with the five testing prey densities. The curves of the proportions of prey consumed by the above predatory stages of *M. sexmaculatus* and *P. dissecta* were similar and took the form of a decelerating type II functional response when the beetles were provided with prey-supply amounts ranging from extremely scarce to abundant. The findings agree with previous studies reported for many insect species (Bayoumy 2011a, 2011b; Omkar and Pervez 2011; Osman and Bayoumy 2011; Gupta *et al.* 2012; Kumar *et al.* 2014a) and are characterised by a curvilinear increase in predation with increase in prey density, becoming asymptotic at high prey densities and thereafter remaining constant due to satiation (Jalali *et al.* 2010).

Furthermore, the logistic regression analysis in the present study indicated a type III response for *P. dissecta* fourth-instar larvae under the scarce and abundant rearing prey densities and for the species' adult females under an optimal rearing prey density, with no plateau observed for the function. However, the proportion of prey consumed (N_e/N_0) by these predators did not increase

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

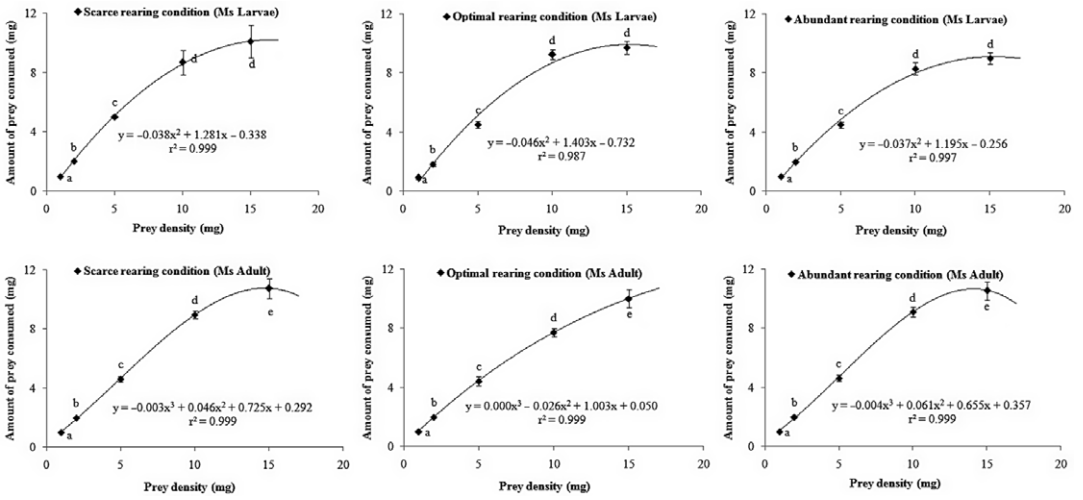


Fig. 1. Fitted relationships for the amount of prey consumed by fourth-instar larvae and adult females of *M. sexmaculatus* (Ms) when provided with five different biomasses of aphid prey. Small letters represent comparison of means between the five prey biomasses.

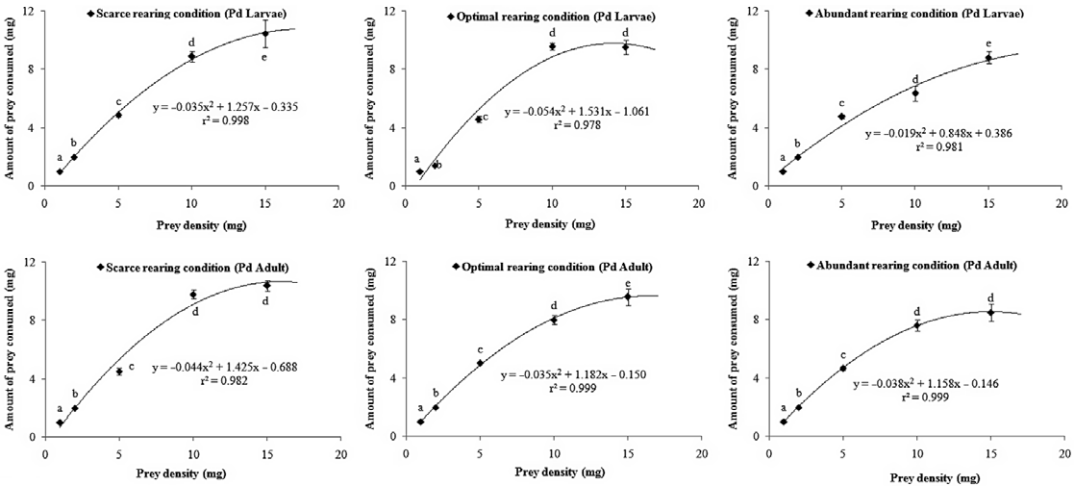


Fig. 2. Fitted relationships for the amount of prey consumed by fourth-instar larvae and adult females of *P. dissecta* (Pd) when provided with five different biomasses of aphid prey. Small letters represent comparison of means between the five prey biomasses.

with increasing prey density, as is generally observed for a type III functional response; instead, it decreased when the biomass of prey provided was increased, similar to the type II functional response. Based on this, the results suggest a modified type II functional response for these predators. Bayoumy (2011b) and Osman and Bayoumy (2011) reported similar results with modified type II functional response curves for the parasitoid *Aphytis diaspidis* Howard and coccinellid predator *Stethorus gilvifrons* Mulsant.

Kumar *et al.* (2014b) also reported modified type II functional response curves when *Coccinella septempunctata* (Linnaeus) and *Coccinella transversalis* Fabricius were kept in conspecific and heterospecific combinations and exposed to increasing biomass of pea aphid. According to

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

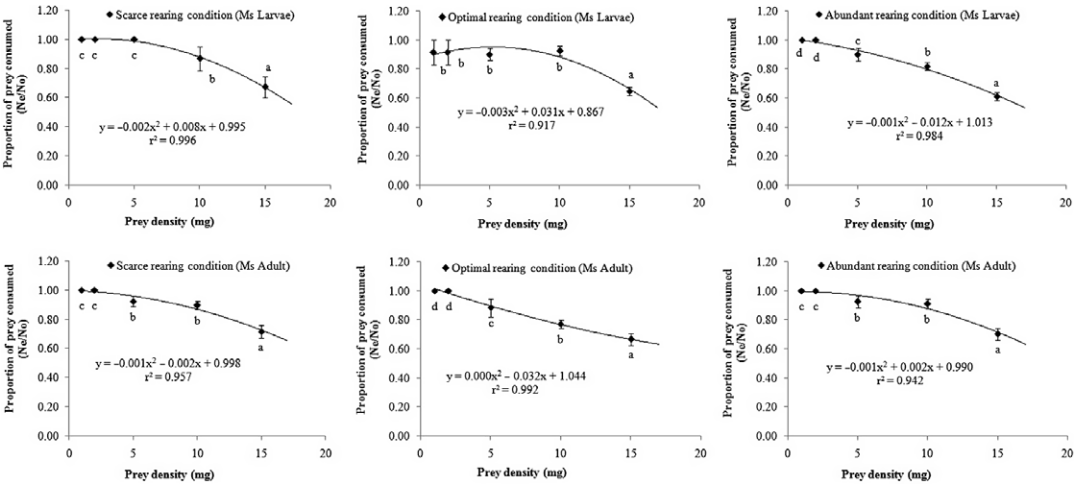


Fig. 3. Fitted relationships for the proportion of prey consumed (N_e/N_0) by fourth-instar larvae and adult females of *M. sexmaculatus* (Ms) when provided with five different biomasses of aphid prey. Small letters represent comparison of means between the five prey biomasses.

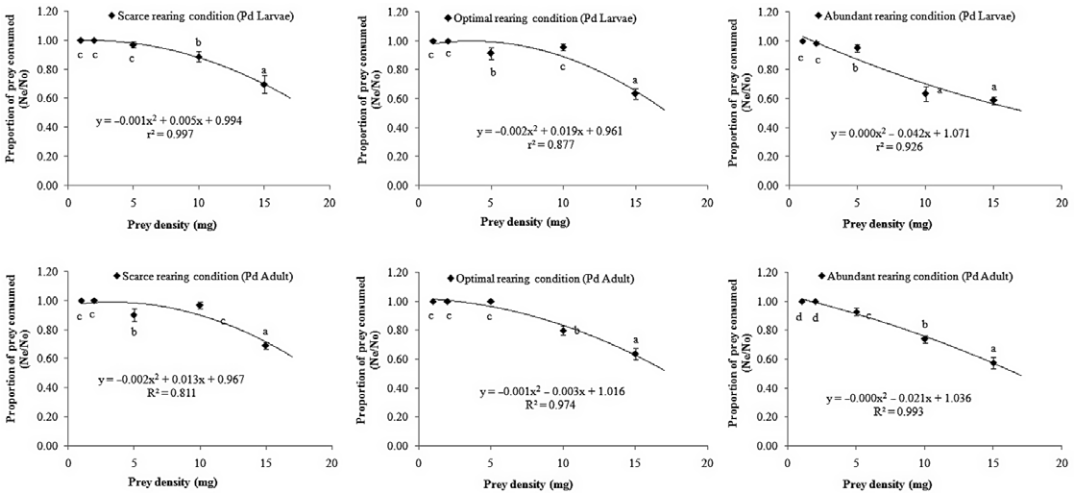


Fig. 4. Fitted relationships for the proportion of prey consumed (N_e/N_0) by fourth-instar larvae and adult females of *P. dissecta* (Pd) when provided with five different biomasses of aphid prey. Small letters represent comparison of means between the five prey biomasses.

Chaudhary *et al.* (2016), females of *M. sexmaculatus* also exhibited modified type II functional response curves when provided with increasing biomass of cowpea aphid. It is highly probable that the functional responses of such predators would be better estimated using more natural arenas like small plants. Using a wider range and number of different prey abundances might also greatly increase the accuracy with which functional responses can be estimated.

Although the attack rate was highest for *M. sexmaculatus* and *P. dissecta* fourth-instar larvae under the optimal rearing prey density, both species' adult females had the highest attack rates under abundant- and scarce-prey rearing conditions, respectively. Furthermore, the fourth-instar larvae and adult females of both species had the shortest prey-handling time (T_h) and the greatest predicted consumption of prey over 24 hours (T/T_h) when reared on the scarce-prey density.

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Table 3. Attack rate and prey-handling time (T_h) for *Menochilus sexmaculatus* and *Propylea dissecta*, derived from their functional response parameters.

Coccinellid species	Stage	Rearing conditions	Attack rate (a)	95% confidence limit		Prey-handling time (hours; T_h)	95% confidence limit		T/T_h (where T = 24 hours)
				Lower	Upper		Lower	Upper	
M. sexmaculatus	Fourth instars	Scarce	0.06 ± 0.04	−0.01	0.14	2.17 ± 0.15	1.87	2.46	11.06
		Optimal	0.25 ± 0.24	−0.24	0.74	2.42 ± 0.08	2.26	2.58	9.91
		Abundant	0.05 ± 0.01	0.03	0.08	2.51 ± 0.08	2.35	2.68	9.56
	Adult females	Scarce	0.05 ± 0.02	0.02	0.08	2.11 ± 0.10	1.90	2.31	11.40
		Optimal	0.03 ± 0.01	0.02	0.05	2.24 ± 0.12	2.00	2.48	10.72
		Abundant	0.06 ± 0.02	0.02	0.10	2.15 ± 0.98	1.95	2.34	11.18
P. dissecta	Fourth instars	Scarce	0.06 ± 0.03	0.00	0.11	2.18 ± 0.13	1.91	2.45	10.99
		Optimal	0.24 ± 0.31	−0.39	0.87	2.45 ± 0.11	2.24	2.66	9.80
		Abundant	0.04 ± 0.01	0.02	0.06	2.80 ± 0.14	2.52	3.07	8.58
	Adult females	Scarce	0.17 ± 0.10	−0.03	0.37	2.30 ± 0.06	2.14	2.40	10.59
		Optimal	0.06 ± 0.02	0.02	0.09	2.46 ± 0.10	2.26	2.66	9.75
		Abundant	0.05 ± 0.02	0.02	0.08	2.73 ± 0.11	2.51	2.95	8.79

These results substantiate the hypothesis that the larvae and adults might have an innate energy accumulation threshold that they try to reach under limited prey availability by investing less time in attacking and consuming the prey compared to their usual predation rates that are displayed under optimal or abundant prey availability. Because environmental unpredictability encourages behavioural flexibility in insects (Dejean *et al.* 2003), the individuals that fed poorly during their early larval stages might accumulate fewer reserves – presumably in the form of stored fat – to carry through pupation into adulthood. As a result, they might feed more aggressively during their late-larval stages or as adults, as demonstrated by higher attack rates and lower prey-handling times.

The fourth-instar larvae of both coccinellid species that had been evaluated earlier for their functional response parameters were assessed again as adults for the same parameters. We found that the *M. sexmaculatus* larvae and adults exhibited similar functional response curves on the three rearing prey densities, whereas the functional response curves of *P. dissecta* larvae differed from those of this species' adult females. Moreover, both species showed lower prey-handling time and higher prey-consumption rates as adults than as larvae. These results further substantiate the hypothesis that the fluctuating-prey densities that coccinellids experience during larval development might modulate the functional response curves of adults and also make the adults more voracious and more efficient in handling prey.

In comparison to *P. dissecta*, the higher prey consumption or functional response curves of *M. sexmaculatus* under the five testing prey densities might be ascribed to certain intrinsic advantages possessed by *M. sexmaculatus* to maintain its stable coexistence. Mishra *et al.* (2011, 2012) reported higher prey-consumption rates of *M. sexmaculatus* over those of *P. dissecta* when the beetles were fed on a constant biomass of *A. pisum*, *Aphis craccivora* Koch, and *Lipaphis erysimi* (Kaltenbach). Omkar *et al.* (2005) reported the intrinsic advantages of *M. sexmaculatus*, in terms of higher reproductive performance, over the other coexisting coccinellid beetles. Mishra *et al.* (2012) established that *M. sexmaculatus* is a better predator than *P. dissecta* is because the former establishes itself earlier in an area of introduction due to its better predation attributes. The present study's findings strengthen the understanding that *M. sexmaculatus* exploits the prey more efficiently under prey resource fluctuation conditions than *P. dissecta* does, thereby making the former a better biocontrol agent of aphid prey than the latter is.

The present study's results suggest that individuals of *M. sexmaculatus* reared on scarce, optimal, or abundant prey densities exhibit type II functional response curves, both as larvae and adults. Individuals of *P. dissecta* reared on scarce or abundant prey densities display modified type II functional response curves as larvae and type II functional response curves as adults, whereas the individuals of *P. dissecta* reared on an optimal-prey density display type II functional response curves as larvae and modified type II functional response curves as adults. The results further substantiate the hypothesis that the scarce rearing prey condition might set the stage for coccinellid beetles to compensate for the earlier shortage of food by consuming higher prey biomass than usual when they suddenly encounter an optimal or abundant prey resource. The larvae and adults might have an innate energy accumulation threshold that they try to reach under scarce-prey availability by feeding more aggressively, with higher attack rates and lower prey-handling time. Furthermore, *M. sexmaculatus* is shown here to have a better compensatory ability to overcome prey resource fluctuations than *P. dissecta* does. As a result, the former would likely behave as a better biological control agent of aphids than the latter would. Field-based studies are needed to confirm these findings.

Acknowledgements. The authors thank the University Grants Commission, Government of India (Letter no. 30-420/2018) for providing financial assistance under UGC-BSR Start-up grant and the Department of Higher Education, Govt. of U.P. India (125/Sattar-4-2010-46(32)/2009 dated January 16 2010) for financial assistance under the Centre of Excellence programme.

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Disclosure. All authors contributed significantly, and all authors are in agreement with the content of the manuscript and have no conflicts of interest.

References

Bayoumy, M.H. 2011a. Foraging behaviour of the coccinellids *Nephus includens* (Coleoptera: Coccinellidae) in response to *Aphis gossypii* (Hemiptera: Aphididae), with particular emphasis on larval parasitism. Environmental Entomology, **40**: 835–843.

Bayoumy, M.H. 2011b. Functional response of the aphelinid parasitoid, *Aphytis diaspidis*: effect of host scale species, *Diaspidiotus perniciosus* and *Hemiberlesia lataniae*. Acta Phytopathological et Entomologica Hungarica, **46**: 101–113.

Bayoumy, M.H. and Michaud, J.P. 2012. Parasitism interacts with mutual interference to limit foraging efficiency in larvae of *Nephus includes* (Coleoptera: Coccinellidae). Biological Control, **62**: 120–126.

Bell, W.J. 1990. Searching behavior patterns in insects. Annual Review of Entomology, **35**: 447–467.

Chaudhary, D.D., Kumar, B., Mishra, G., and Omkar. 2015. Resource partitioning in a ladybird, *Menochilus sexmaculatus*: function of body size and prey density. Bulletin of Entomological Research, **105**: 121–128.

Chaudhary, D.D., Kumar, B., Mishra, G., and Omkar. 2016. Effects of prey resource fluctuation on predation attributes of two sympatric ladybird beetles. The Canadian Entomologist, **148**: 443–451.

Dejean, A., Gibernau, M., Lauga, J., and Orivel, J. 2003. Coccinellid learning during capture of alternative prey. Journal of Insect Behaviour, **16**: 859–864.

Dixon, A.F.G. 2000. Insect predator-prey dynamics: ladybird beetles and biological control. First edition. Cambridge University Press, London, United Kingdom. 257 pp.

Dukas, R. 2008. Evolutionary biology of insect learning. Annual Review of Entomology, **53**: 145–160.

Fathipour, Y., Hosseini, A., Taleb, A., and Moharramipour, S. 2006. Functional response and mutual interference of *Diaeretiella rapae* (Hymenoptera: Aphidiidae) on *Brevicoryne brassicae* (Homoptera: Aphididae). Entomologica Fennica, **17**: 90–97.

Giurfa, M. 2013. Cognition with few neurons: higher-order learning in insects. Trends in Neurosciences, **36**: 285–294.

Giurfa, M. 2015. Learning and cognition in insects. Wiley Interdisciplinary Reviews: Cognitive Science, **6**: 383–395.

Grez, A.A., Viera, B., and Soares, A.O. 2012. Biotic interactions between *Eriopis connexa* and *Hippodamia variegata*, a native and an exotic coccinellids species associated with alfalfa fields in Chile. Entomologia Expermentalis et Applicata, **142**: 36–44.

Grez, A.A., Zaviezo, T., and Mancilla, A. 2011. Effect of prey density on intraguild interactions among foliar-and ground-foraging predators of aphids associated with alfalfa crops in Chile: a laboratory assessment. Entomologia Expermentalis et Applicata, **139**: 1–7.

Gupta, R.K., Pervez, A., Guroo, M.A., and Srivastava, K. 2012. Stage-specific functional response of an aphidophagous ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae), to two aphid species. International Journal of Tropical Insect Science, **32**: 136–141.

Hassell, M.P. 1978. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, New Jersey, United States of America. 237 pp.

Hiltunen, T. and Laakso, J. 2013. The relative importance of competition and predation in environment characterized by resource pulses: an experimental test with a microbial community. BMC Ecology, **13**: 1–8.

Hodek, I. and Honek, A. 1996. Ecology of coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands. 464 pp.

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Hodek, I., Van Emden, H.F., and Honek, A. 2012. Ecology and behaviour of the ladybird beetles (Coccinellidae). John Wiley and Sons, West Sussex, United Kingdom. 600 pp.

Jalali, M., Tirry, L., and De Clercq, P. 2010. Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*. BioControl, **55**: 261–269.

Jamour, T.K. and Shishehbor, P. 2012. Host plant effects on the functional response of *Stethorus gilvifrons* to strawberry spider mites. Biocontrol Science and Technology, **22**: 101–110.

Juliano, S.A. 2001. Nonlinear curve fitting: predation and functional response curves. Design and Analysis of Ecological Experiments, **2**: 178–196.

Kumar, B., Bista, M., Mishra, G., and Omkar. 2014a. Stage specific consumption and utilization of aphids conspecific and heterospecific eggs by two species of *Coccinella* (Coleoptera: Coccinellidae). European Journal of Entomology, **111**: 363–369.

Kumar, B., Mishra, G., and Omkar. 2014b. Functional response and predatory interactions within conspecific and heterospecific guilds of two congeneric species (Coleoptera: Coccinellidae). European Journal of Entomology, **111**: 257–265.

Mishra, G., Kumar, B., Shahid, M., Singh, D. and Omkar. 2011. Evaluation of four co-occurring ladybirds for use as biocontrol agents of pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). Biocontrol Science and Technology, **21**: 991–997.

Mishra, G., Omkar, Kumar, B., and Pandey, G. 2012. Stage- and age-specific predation in four aphidophagous ladybird beetles. Biocontrol Science and Technology, **22**: 463–476.

Mondor, E.B. and Warren, J.L. 2000. Unconditioned and conditioned responses to colour in the predatory coccinellid, *Harmonia axyridis* (Coleoptera: Coccinellidae). European Journal of Entomology, **97**: 463–467.

Moreyra, S. and Lozada, M. 2021. How behavioral plasticity enables foraging under changing environmental conditions in the social wasp *Vespula germanica* (Hymenoptera: Vespidae). Insect Science, **28**: 231–237.

Ninkovic, V. and Pettersson, J. 2003. Searching behaviour of the seven-spotted ladybird, *Coccinella septempunctata*: effects of plant odour interaction. Oikos, **100**: 65–70.

Omkar and Pervez, A. 2000. Biodiversity of predaceous coccinellids (Coleoptera: Coccinellidae) in India: a review. Journal of Aphidology, **14**: 41–67.

Omkar and Pervez, A. 2011. Functional response of two aphidophagous ladybirds searching in tandem. Biocontrol Science and Technology, **21**: 101–111.

Omkar, Mishra, G., Kumar, B., Singh, N., and Pandey, G. 2014. Risk associated with tandem release of large and small ladybird (Coleoptera: Coccinellides) in heterospecific aphidophagous guilds. The Canadian Entomologist, **146**: 52–66.

Omkar, Mishra, G., Srivastava, S., Gupta, A.K., and Singh, S.K. 2005. Reproductive performance of four aphidophagous ladybirds on cowpea aphid, *Aphis craccivora* Koch. Journal of Applied Entomology, **129**: 217–220.

Osman, M.A. and Bayoumy, M.H. 2011. Effect of prey stages of the two-spotted mite *Tetranychus urticae* on functional response of the coccinellids predator *Stethorus gilvifrons*. Acta Phytopathologica et Entomologica Hungarica, **46**: 277–288.

Ostfeld, R.S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution, **15**: 232–237.

Papaj, D.R. and Lewis, A.C. 2012. Insect learning: ecology and evolutionary perspectives. Springer Science and Business Media, Berlin, Germany. 398 pp.

Patel, P., Kumar, B., and Kumar, D. 2017. Fluctuations in defended prey availability modulate the functional response curves of *Menochilus sexmaculatus* (Coleoptera: Coccinellidae). Acta Entomologica Sinica, **60**: 1031–1040.

Remén, C. 2004. Associated learning of colour and odour in the seven-spotted ladybird *Coccinella septempuncata* (L.): an olfactometer experiment [online]. Institutionen för entomologi, Sveriges lantbruksuniv. Available from https://stud.epsilon.slu.se/12721/1/remen_c_171019.pdf (accessed 12 October 2020).

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press

Roger, D. 1972. Random search and insect population models. The Journal of Animal Ecology, **41**: 369–383.

Santos-Cividanes, T.M., Dos Anjos, A.C.R., Cividanes, F.J., and Dias, P.C. 2011. Effects of food deprivation on the development of *Coleomegilla maculata* (De Geer) (Coleoptera: Coccinellidae). Neotropical Entomology, **40**: 112–116.

Snyder, W.E. 2009. Coccinellids in diverse communities: which niche fits? Biological Control, **51**: 323–335.

Snyder, W.E. and Ives, A.R. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. Ecology, **84**: 91–107.

Vanaclocha, P., Papacek, D., Monzo, C., Verdu, M.J., and Urbaneja, A. 2013. Intraguild interactions between the parasitoid *Aphytis lingnanensis* and the predator *Chilocorus circumdatus*: implications for the biological control of armoured scales. Biological Control, **65**: 169–175.

Vet, L.E. and Dicke, M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annual Review of Entomology, **37**: 141–172.

Cite this article: Chaudhary, D.D., Kumar, B., Mishra, G., and Omkar, 2022. Functional response in coccinellid beetles (Coleoptera: Coccinellidae) is modified by prey-density experience. The Canadian Entomologist. https://doi.org/10.4039/tce.2021.59.

https://doi.org/10.4039/tce.2021.59 Published online by Cambridge University Press