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FUNCTIONAL RESPONSE- A FUNCTION OF PREDATOR AND PREY SPECIES

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ABSTRACT

The functional response types and parameters of 4th instar larvae, adult females and males of coccinellid predators, *Adalia tetraspilota* (Hope) and *Hippodamia variegata* (Goeze) were evaluated at five different densities of *Aphis pomi* De Geer, *Brevicoryne brassicae* (Linnaeus) and *Aphis craccivora* Koch in order to understand the effect of predator species and stage, and prey species on functional response and to understand their role for the aphids' biological control. Experiments were carried out in petri dishes at 25 ± 2°C and 65 ± 5% R.H. and 14L: 10D photoperiod in a controlled environment room. All tested stages exhibited a Type II response. The attack rate (*a*) and handling time (T_h) coefficients differed for various growth stages of each predator and for the three prey species tested. So did the parameter values for the two predators indicating that various predatory stages of a predator have different abilities to respond to increasing prey densities, so do the various predators for a particular prey species and a particular predator towards various prey species. Attack rate coefficients didn't differ as much as the handling time, thus re-establishing the fact that handling time is a good indicator of the effectiveness of a predator.

INTRODUCTION

Predation is assumed to be one of the significant biotic mortality factors reducing insect pest populations, and their use in insect pest management programs has received increased attention because of the current need to reduce the exclusive use of insecticides for pest control (Atlihan *et al.*, 2010). 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). Ecologists have delimited functional response into three types (Holling 1959, 1966). The functional response curves may represent an increasing linear relationship (Type I), a decelerating curve (Type II), or a sigmoid relationship (Type III). This could further be simplified in terms of density independence. 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. 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. The usefulness of logistic regression model for determining the type of functional response has been aptly dealt with by Pervez and Omkar (2005).

Ladybird beetles (Coccinellidae: Coleoptera) are important predators in natural and agricultural habitats and prey upon many economically important pests, including aphids, mealy bugs, scale insects, thrips, leaf hoppers, mites and other soft bodied insects (Dixon, 2000). *Adalia tetraspilota* (Hope) and *Hippodamia (Adonia) variegata* (Goeze) are the predominant species of coccinellids in agro-ecosystems of Kashmir valley (Khan *et al.*, 2007). *H. variegata* originated in the Palearctic region (Gordon, 1987) and is a widespread predator of aphids in many parts of the world (Franzmann 2002). This species is considered the most important natural enemy of aphids in many countries including Bulgaria, Ukraine, Italy, India and Turkmenistan (Kontodimas and Stathas 2005). *A. tetraspilota* is most abundant predatory coccinellid in Kashmir and has been observed feeding on *Aphis pomi* De Geer, *Myzus persicae* Harris, *Lipaphis erysimi* (Kaltenbach), *Brevicoryne brassicae* (Linnaeus), *Aphis fabae* Scopoli, *Aphis craccivora* Koch, etc. (Khan *et al.*, 2009). As aphids are regular pests in temperate zone, the functional response and biocontrol potential of the aforementioned coccinellids was evaluated to three pest aphid species, namely *A. pomi*, *A. craccivora* and *B. brassicae*. The investigation was carried out to determine relative impact of prey and predator species, and growth stages of the predator on various parameters of functional response, besides to determine the potential role of the predator species for managing the aphid pests.

The functional responses of various predatory stages of the two coccinellids on three aphid species were determined to throw some light on such aspects of functional response as i) whether the functional responses differ among predators when they feed on same prey? (ii) are the functional responses for each predator different when they feed on different prey? (iii) how do the functional response parameters vary with different predatory stages of same or different predator species on various prey species? iv) what is the potential role of these predators for managing the aphid pests?

MATERIALS AND METHODS

Insect rearing

To rear the predator coccinellids, aphid colonies were maintained on fresh twigs of apple, and potted seedlings of kale and cowpea, respectively for *A. pomi*, *B. brassicae* and *A. craccivora* in cages (18x18x18 cm). The colonies were collected from pesticide free apple orchard/ vegetable fields in the University Campus. Ladybeetle cultures were initiated by collecting the newly emerged overwintering adults of the respective coccinellid species. The adults of the two coccinellid species were maintained in plastic jars (height 20 cm and diameter 15 cm) with an abundant supply of prey from the aphid colonies till oviposition. The rearing jars were provided with crumpled paper to act as oviposition sites. The eggs laid were collected every 24 hours and transferred to petri dishes for the proposed studies. All the cultures were maintained at a temperature of 25 ± 2°C and 65 ± 5% relative humidity with a photoperiod of 14:10 light and dark hours in controlled environment rooms. Newly emerged larvae of both the predators were taken from the stock cultures and fed an abundant supply of aphids. The mixed diet was provided to avoid food adaptation (Rana *et al.*, 2002). Adults from this stock were sexed and allowed to mate and the eggs thereof were incubated and the first instar larvae were used for the proposed studies. Newly emerged larvae were fed separately with *ad libitum* supply of 3rd or 4th instar nymphs of the three aphid species.

The functional response of 4th larval instar and adult male and female of *A. tetraspilota* and *H. variegata* to three aphid species namely, *A. pomi*, *A. craccivora* and *B. brassicae* was determined. The larvae and adults were starved for 24 hours in vials individually before the experiments to minimize individual hunger levels as suggested by Nakamura (1977). Five aphid densities were used to work out the functional response i.e. 10, 20, 40, 80 and 160 for all the three species of aphids. The predators were introduced individually into the petri plates containing definite number of aphids per petri dish on excised leaves of respective host plants stuck to agar medium. The aphids were introduced before the predators so that they could disperse and the predators may have to search for the aphids

The aphid densities 10 and 20 were replicated 15 times for each instar of both the predators while as the aphid densities 40, 80 and 160 were replicated only 10 times. Greater number of replications was allocated to lowest two densities to obtain more precise information about the initial part of the functional response curve. One treatment was also designed for natural mortality of the aphids. After 24 hours, the number of aphids consumed by the various instars of the predators was recorded by counting the remaining number of aphids present in each petri dish.

Statistical analysis

Prior to fitting the data to a particular Hollings' equation (Holling, 1959 and 1966), it's important to know the type of functional response exhibited by a particular instar of a predator to a particular prey species. Logistic regression model is such a tool that is used to determine the shape (type) of functional response by taking into consideration the proportion of prey eaten (N_a/N_0) as a function of prey offered (N_0) (Juliano, 2001). Hence the data was fitted to the following polynomial function that describes the relationship between N_a / N_0 and N_0:

$$\frac{Na}{N_0} = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_2N_0^3)}{1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_2N_0^3)}$$

Where,

P_0 = Intercept

P_1 = Linear coefficient

P_2 = Quadratic coefficient

P_3 = Cubic coefficient

N_a = Number of prey eaten

N_o = Number of prey offered.

The coefficients are 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). The coefficients of polynomial logistic regression were determined using the function "glm" in R-software (R Development Core Team, 2008).

After the determination of type of functional response, the data i.e. the number of aphids preyed upon by different stages of coccinellids at different densities was analysed by fitting Rogers' Type II Random Predator Equation (Rogers, 1972) with the help of non-linear least square regression to determine the parameters of functional response.

Rogers type II Random Predator Equation is given by
$N_a = N_o (1 - \exp [a (T_h N_a - T)])$

Where,

N_a = Number of prey eaten

N_o = Number of prey offered

a = attack rate

T_h = handling time

T = time of confinement (24 hours)

To determine the coefficients of attack rate and handling time using non-linear least square regression as suggested by Rogers (1972), the function "nls" provided by the R-software was used (R Development Core Team, 2008).

After a and T_h were determined for the original data (m_t), the differences among a values, as well as T_h values, were tested for significance by estimating the variance using the jackknife technique (Meyer *et al.*, 1986). The Jackknife pseudo-value (m_j) was calculated for the n samples using the following equations:

$m_{ja} = n.m_{ta} - (n-1)m_{ia}$

$m_{jTh} = n.m_{tTh} - (n-1)m_{iTh}$

The mean values of (n–1) jackknife pseudo-values for *a* and T_h for each prey stage were subjected to analysis of variance followed by Least Significant Difference Test ($p \leq 0.01$) (R Development Core Team, 2008).

RESULTS

Prey consumption rates and nature of functional response

The prey consumption rates of 4th instar larvae and adult male and female individuals of the coccinellids predators, *A. tetraspilota* and *H. variegata* on three aphid species viz. *A. pomi*, *A. craccivora*, and *B. brassicae* are presented in Figure 1 and 2. A perusal of the data indicates that the predatory growth stages of both the predators consume *A. craccivora* nymphs the most, followed by *B. brassicae* and *A. pomi*. Among the various predatory stages of *A. tetraspilota* used, the aphid consumption was recorded as maximum by the 4th instar larvae followed by the adult female on all the three prey species used. Same trend was noted for *H. variegata*. The predatory stages of *H. variegata* consumed more number of aphids per day as compared to those of *A. teraspilota*. Percentage of prey consumed by all predatory stages decreased as the offered prey density increased on all the prey species used for both the predators. The percentage of prey consumed declined monotonically with increasing prey density. The graphical analysis of percentage of prey consumed versus offered prey density suggested type II functional response for all the predatory stages. It was further confirmed by the estimates of logistic regression model. The linear coefficient of logistic regression model consistently assumed significant negative (<0) values for all the growth stages of both the predators on all the three prey species (Table 1 and 2).

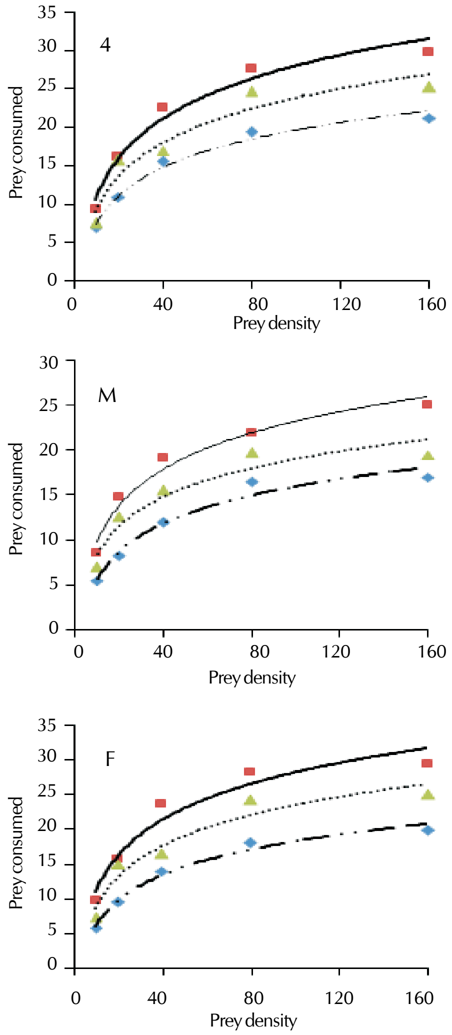

Figure 1: Prey consumption versus prey density offered for various growth stages of *Adalia tetraspilota* on three aphid species;. 4 refers to 4th instar larvae and M, F for adult male and female of *A. tetraspilota*. ■ =*Aphis craccivora*, ▲ = *Brevicoryne brassicae*, ◆ = *A. pomi*.

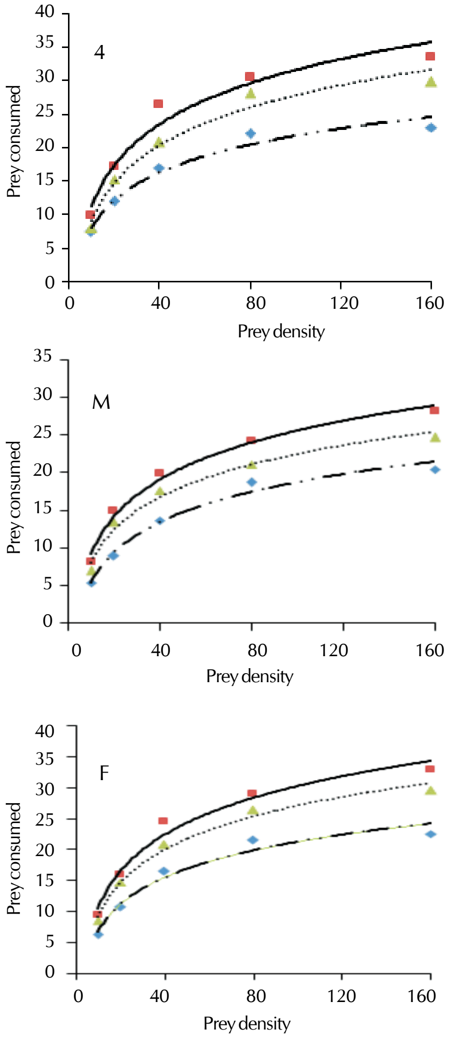

Figure 2: Prey consumption versus prey density offered for various growth stages of *Hippodamia variegata* on three aphid species; 4 refers to 4th instar larvae and M, F for adult male and female of *H. variegata*. ■ = *Aphis craccivora*, ▲ = *Brevicoryne brassicae*, ◆ = *A. pomi*.

Table 1. Maximum likelihood estimates from logistic regression analysis of the proportion of prey eaten by different stages of *Adalia tetraspilota* against initial number of aphids offered.

Prey species	Growth stage	Parameters	Estimates	S.E.	Z value	*Pr* (Z)
B. brassicae	Fourth instar	Intercept	2.704	1.158	2.335	0.0196
		Linear	-1.149e-01	6.339e-02	-1.812	0.0700
		Quadratic	1.224e-03	9.086e-04	1.347	0.1779
		Cubic	-4.232e-06	3.497e-06	-1.210	0.2263
	Adult male	Intercept	1.707	1.025	1.666	0.0956
		Linear	-7.904e-02	5.850e-02	- 1.351	0.1766
		Quadratic	7.414e-04	8.567e-04	0.865	0.3868
		Cubic	-2.445e-06	3.334e-06	-0.733	0.4634
	Adult female	Intercept	2.430	1.112	2.185	0.0289
		Linear	-1.062e-01	6.164e-02	-1.722	0.0850
		Quadratic	1.127e-03	8.887e-04	1.269	0.2046
		Cubic	-3.904e-06	3.431e-06	-1.138	0.2551
A. pomi	Fourth instar	Intercept	1.399	9.970e-01	1.403	0.161
		Linear	-6.861e-02	5.750e-02	-1.193	0.233
		Quadratic	6.239e-04	8.457e-04	0.738	0.461
		Cubic	-2.019e-06	3.297e-06	-0.612	0.540
	Adult male	Intercept	6.656e-01	9.697e-01	0.686	0.492
		Linear	-5.800e-02	5.766e-02	- 1.006	0.314
		Quadratic	5.685e-04	8.587e-04	0.662	0.508
		Cubic	-1.970e-06	3.367e-06	-0.585	0.558
	Adult female	Intercept	6.951e-01	9.627e-01	0.722	0.470
		Linear	-4.520e-02	5.651e-02	-0.800	0.424
		Quadratic	3.476e-04	8.379e-04	0.415	0.678
		Cubic	-1.054e-06	3.279e-06	-0.321	0.748
A. craccivora	Fourth instar	Intercept	4.180	1.548	2.700	0.00693
		Linear	-1.557e-01	7.875e-02	- 1.978	0.04798
		Quadratic	1.637e-03	1.086e-03	1.507	0.13184
		Cubic	-5.530e-06	4.104e-06	-1.348	0.17780
	Adult male	Intercept	2.726	1.192e+00	2.288	0.0222
		Linear	-1.037e-01	6.461e-02	-1.604	0.1087
		Quadratic	9.609e-04	9.234e-04	1.041	0.2981
		Cubic	-3.034e-06	3.551e-06	-0.854	0.3930
	Adult female	Intercept	3.670	1.456	2.520	0.0117
		Linear	-1.272e-01	7.508e-02	-1.695	0.0902
		Quadratic	1.252e-03	1.044e-03	1.200	0.2302
		Cubic	-4.114e-06	3.956e-06	-1.040	0.2983

The handling time (T_h) and attack rate (*a*) are the parameters that reflect the significance of functional response. As the polynomial logistic regression model suggested the type II functional response for all the predatory stages, the data on predation rates was fitted to the random predator equation to estimate the handling time (T_h) and attack rate (*a*). The estimates are presented in Table 3 and 4. Among the three predatory stages, lowest T_h was exhibited by 4th instar larvae followed by adult female in most of the cases, except for *H. variegata* on *B. Brassicae* and *A. Craccivora* in which case the trend was reverse. Higher attack rates were possessed by 4th instar larvae in all the cases except for *A. tetraspilota* on *A. craccivora* in which case adult females possessed the highest attack rate followed by 4th instar larvae. In all cases, adult males possessed the highest handling time and lowest attack rate as compared to other predatory stages.

DISCUSSION

Prey consumption rates and nature of functional response

A perusal of the data on prey consumption rates of various predatory stages of *Adalia tetraspilota* and *Hippodamia variegata* indicated that the 4th instar larvae of both the predators consumed highest number of aphids, irrespective of the prey species, closely followed by the adult females. The observation that 4th instar larvae consumed greatest proportion of prey over 24 hours, consuming over 60% of total prey consumed by all the larval stages, is consistent with the observations of many other workers on the same and other coccinellids like those of Farhadi *et al*. (2010) for *H. variegata* preying upon *A. fabae*; Khan (2009) for *A. tetraspilota* preying upon *B. brassicae*; Khan (2010) for *Harmonia eucharis* preying upon *Aphis pomi*; Lee and Kang (2004) for *H. axyridis* preying upon *Aphis gossypii*, to mention a few. As pointed out by Jervis *et al* (2005), final instar larva accounts for more than 75 % of total growth that occurs in predaceous coccinellids, cumulative increase in prey biomass consumed reaches its peak in 4th instar larvae for coccinellids. The higher prey consumption rates of adult females may be due to a higher nutrient requirement for special purposes such as egg production, or due to delayed satiation (Mills, 1982) or due to possible faster digestive rate of adult females (Pervez and Omkar, 2005). Bedddington *et al*. (1976) pointed out that variation in prey consumption rates could be expected from the between-instar differences that exist with respect to attack

Table 2. Maximum likelihood estimates from logistic regression analysis of the proportion of prey eaten by different stages of *Hippodamia variegata* against initial number of aphids offered.

Prey species	Growth stage	Parameters	Estimates	S.E.	Z value	*Pr* (Z)
A. pomi	Fourth instar	Intercept	1.683	1.026	1.641	0.101
		Linear	-7.432e-02	5.829e-02	-1.275	0.202
		Quadratic	7.007e-04	8.510e-04	0.823	0.410
		Cubic	-2.323e-06	3.305e-06	-0.703	0.482
	Adult male	Intercept	5.442e-01	9.602e-01	0.567	0.571
		Linear	-4.241e-02	5.648e-02	-0.751	0.453
		Quadratic	3.529e-04	8.374e-04	0.421	0.673
		Cubic	-1.150e-06	3.276e-06	-0.351	0.726
	Adult female	Intercept	8.776e-01	9.679e-01	0.907	0.365
		Linear	-4.110e-02	5.603e-02	-0.733	0.463
		Quadratic	2.887e-04	8.252e-04	0.350	0.726
		Cubic	-8.554e-07	3.218e-06	-0.266	0.790
B. brassicae	Fourth instar	Intercept	2.396	1.155	2.075	0.038
		Linear	-8.507e-02	6.300e-02	-1.350	0.177
		Quadratic	8.026e-04	9.012e-04	0.891	0.373
		Cubic	-2.638e-06	3.465e-06	-0.761	0.446
	Adult male	Intercept	1.622	1.032	1.572	0.116
		Linear	-6.254e-02	5.836e-02	-1.072	0.284
		Quadratic	4.980e-04	8.514e-04	0.585	0.559
		Cubic	-1.625e-06	3.308e-06	-0.491	0.623
	Adult female	Intercept	2.591	1.183	2.191	0.0285
		Linear	-9.416e-02	6.413e-02	-1.468	0.1420
		Quadratic	8.922e-04	9.151e-04	0.975	0.3296
		Cubic	-2.893e-06	3.515e-06	-0.823	0.4103
A. craccivora	Fourth instar	Intercept	4.161	1.696e	2.453	0.014
		Linear	-1.310e-01	8.509e-02	-1.540	0.123
		Quadratic	1.221e-03	1.164e-03	1.049	0.294
		Cubic	-3.851e-06	4.377e-06	-0.880	0.378
	Adult male	Intercept	2.498e	1.169e	2.136	0.032
		Linear	-8.892e-02	6.362e-02	-1.398	0.162
		Quadratic	7.826e-04	9.101e-04	0.860	0.389
		Cubic	-2.403e-06	3.501e-06	-0.686	0.492
	Adult female	Intercept	3.366	1.415	2.378	0.017
		Linear	-1.079e-01	7.353e-02	-1.467	0.142
		Quadratic	9.803e-04	1.026e-03	0.955	0.339
		Cubic	-3.065e-06	3.896e-06	-0.787	0.431

Table 3. Estimates of attack rate (*a*) for various growth stages of *A. tetraspilota* and *H. variegata* preying upon *A. pomi*, *B. brassicae* and *A. craccivora* for random predator equation.

Predator	Prey species	Predatory stage	Estimate	S.E	t-value	Pr(t)
A. tetraspilota	*A. pomi*	4th Instar	0.06413	0.0036	17.34	0.0004
		Adult male	0.04266	0.0132	3.233	0.0481
		Adult female	0.05082	0.0036	13.99	0.0079
	B. brassicae	4th Instar	0.07899	0.00369	17.34	0.00041
		Adult male	0.07441	0.01320	3.233	0.04811
		Adult female	0.07361	0.00363	13.99	0.00079
	A. craccivora	4th Instar	0.12715	0.00849	15.01	0.00064
		Adult male	0.08081	0.01325	6.09	0.00885
		Adult female	0.17437	0.02259	7.71	0.00452
H. variegata	*A. pomi*	4th Instar	0.08117	0.02054	5.006	0.01530
		Adult male	0.04579	0.00864	7.158	0.00561
		Adult female	0.07006	0.00430	19.95	0.00027
	B. brassicae	4th Instar	0.10279	0.01797	4.518	0.0203
		Adult male	0.06186	0.006889	6.648	0.00693
		Adult female	0.08592	0.01732	4.044	0.0272
	A. craccivora	4th Instar	0.14429	0.01341	10.76	0.0017
		Adult male	0.07147	0.01086	6.66	0.0068
		Adult female	0.10671	0.01127	9.46	0.0025

Table 4. Estimates of handling time (T_h) for various growth stages of *A. tetraspilota* and *H. variegata* preying upon *A. pomi*, *B. brassicae* and *A. craccivora* for random predator equation.

Predator	Prey species	Predatory stage	Estimate	S.E	t-value	Pr(t)
A. tetraspilota	*A. pomi*	4th Instar	1.02057	0.0083	122.29	1.21e-06
		Adult male	1.23514	1.0668	18.488	0.00034
		Adult female	1.07765	0.0129	83.21	3.83e-06
	B. brassicae	4th Instar	0.84967	0.00834	122.29	1.21e-06
		Adult male	1.11832	0.06681	18.48	0.00034
		Adult female	0.85564	0.01295	83.21	3.83e-06
	A. craccivora	4th Instar	0.75051	0.00480	156.20	5.79e-07
		Adult male	0.87878	0.01902	46.21	2.23e-05
		Adult female	0.77261	0.00680	113.58	1.50e-06
H. variegata	*A. pomi*	4th Instar	0.95328	0.01779	41.29	3.13e-05
		Adult male	1.01693	0.02088	41.41	3.1e-05
		Adult female	0.96121	0.00536	136.8	8.6e-07
	B. brassicae	4th Instar	0.73441	0.02523	37.788	4.08e-05
		Adult male	0.86497	0.029934	33.972	5.61e-05
		Adult female	0.73326	0.03253	29.551	8.51e-05
	A. craccivora	4th Instar	0.66856	0.00593	112.60	1.54e-06
		Adult male	0.75444	0.01914	39.48	3.57e-05
		Adult female	0.66733	0.00912	73.14	5.63e-06

rate and handling time (parameters of functional response), and metabolic rate, which increases with development.

Among the two coccinellid predators used in the study, the predatory stages of *H. variegata* consistently consumed more number of prey individuals as compared to *A. tetraspilota*. The elevated prey consumption curves for *H. variegata* over that of *A. tetraspilota* indicated a possible delayed satiation and/or a possible faster digestive rate in case of the former. Pervez and Omkar (2005) speculated that the elevated functional response curve of *Cheilomenes sexmaculata* over *Coccinella transversalis* may be a result of such differences. Isikber (2004) found that large sized aphidophagous predators consumed comparatively more aphids than small sized species.

The variation in prey consumption rates of a predator on various prey species is attributed to various factors such as prey mobility (Dixon, 2000), nutritional status (Thompson, 1999), suitability of the prey for the growth and reproduction of the predator (Hodek and Honek, 1996), prey size (Isikber, 2004), effect of host plant of prey (Wu *et al*., 2010), etc. As *A. craccivora* was reared on a legume host, it is expected to possess a higher percentage of protein nitrogen which could possibly make it a comparatively more preferred prey (Atwal and Sethi, 1963).Some or all the mentioned factors could probably account for observed variation in prey consumption rates of *H. variegata* and *A. teraspilota*.

The current study revealed the estimates of maximum number of aphids attacked per day as 33.5 for 4th instar larvae and 32.8 for adult females of *H. variegata* when *A. craccivora* was used as prey. Rest of the predatory stages of both the predator species consumed lower numbers of prey individuals in the speculated period of time on any of the three aphid prey species used. The results are consistent with those of Khan and Mir (2008) who reported the maximum prey consumption in the range of 15-30 aphids per day for adult females of coccinellid species *A. tetraspilota*, *Coccinella septumpunctata*, *Calvia punctata* and *H. variegata* preying upon *B. brassicae*, and Khan (2009) with all predaceous stages of *Harmonia eucharis* preying upon *A. pomi*. However, all these estimates are considerably lower than those reported by other workers from other parts of the world working with same coccinellid species. Jafari and Shoushtari (2010) reported maximum consumption by 4th instar larvae of *H. variegata* as 52.78 preying upon *A. fabae*. Saleh *et al*. (2010) reported a maximum consumption of 147.06 aphids per day for the adult females of *H. variegata* upon *Brcahycaudus helichrysi*. Jafari and Goldasteh (2009) reported the estimate of maximum prey consumption for *H. variegata* as 135.29 preying upon *A. fabae*. Similar results were found for *Adalia bipunctata* preying upon various aphid species (Omkar and Pervez, 2005). Other than the effects of prey species in terms of its nutritional status and possible tritrophic interactions of prey host plant on the predator, another very important factor that may be responsible for the variation in various biological and predation parameters is the geographical variation in the populations of the coccinellid predators (Kontodimas and Stathas, 2005). As suggested by Dobzhansky (1933), the geographical variability produces differences in the populations of coccinellid predators with respect to various biological and ecological parameters.

The graphical analysis of per cent prey consumption (trend-line analysis) and the results of polynomial logistic regression revealed that a type II asymptotic curve described the data well. The logistic regression model increases the credibility of the correctness of the curves, as in such studies ecologists normally face difficulties in curve-fitting when the data set of type II responses shows inclination towards type III response which can lead to drawing of misleading inferences (Pervez and Omkar, 2005). Higher number of replications for the lowest two offered prey densities in the first instance and subsequent curve-fitting using the polynomial logistic regression were hence used to take care of such apprehensions.

Out of the three types of functional responses identified by Holling (1959), only type III produces density dependent mortality that is thought to regulate target populations. The only possibility of exhibiting type III functional response in the present study is the concentration of predator hunting in high-density patches (Farhadi *et al*., 2010). The mechanism may have operated in the current study, however no evidence of type III functional response was found for the predator-prey complexes under study. The other mechanisms of type III response i.e. switching behaviour and predator learning could not have operated as the experiments were short term and single prey based.

Parameters of functional response

The coefficient of attack rate (*a*) and handling time (T_h) were the parameters used to find out the magnitude of the functional responses exhibited by the predatory stages of *A. tetraspilota* and *H. variegata* on the three prey species, namely *A. pomi*, *A. craccivora* and *B. brassicae*. Their values differed for various growth stages of each predator and for the three prey species tested. So did the parameter values for the two predators. It indicates that various predatory stages of a predator have different abilities to respond to increasing prey densities, so do the various predators for a particular prey species and a particular predator towards various prey species. These results are in conformation with those of Pervez and Omkar (2005) who investigated the functional responses of *Cheilomenes sexmacvulta* (F.), *Propylea dissecta* (M.) and *Cocccinella transversalis* F. adults on *Myzus persicae* (Sulzer) and *A. craccivora*. The differences in the parametric values might be due to variation in size, voracity, satiation time, digestion ability, walking speed, etc. (Mills, 1982; Pervez and Omkar. 2005).

In general, attack rate coefficients obtained in the various treatments don't differ as much as those of the handling time. Jackknife technique revealed insignificant variation in attack rate among the predatory stages on various prey species ($F = 1.7345$; d.f. = 17, 68; $P=0.05722$) while as the handling time showed significant variation ($F = 6.3051$; d.f. = 17, 68; $P<0.0001$). This observation is consistent with that of Atlihan *et al.* (2010) Atlihan *et al.* (2010) and Pervez and Omkar (2005). The handling time is a good indicator of consumption rate and effectiveness of a predator because it reflects the cumulative effect of time taken during capturing, killing, subduing and digesting the prey (Veervel and Baskaran, 1997).

The practical implication of these studies is that 4th instar larvae and females are the stages that are most effective as predators. It may be suggested that mass release of the predators in question may be most effective if releases are done primarily as last stage individuals (4th instars and adult females). Such releases would facilitate rapid killing of prey immediately after release. The sex ratio of mass produced ladybeetles if made to favour female individuals may be advantageous for biological control as adult females and 4th instar larvae are better in devouring of aphid prey. Among the two predator species, *H. variegata* is better as a bioagent as per the laboratory studies and among the prey species tested, the predators may respond best to the patches of *A. craccivora*. However, the prey consumption rates are comparatively lower besides the uncontrolled and highly variable field conditions could radically change functional response of the predators (Farhadi *et al.*, 2010). Other factors such as intrinsic growth rates, host patchiness, predation and competition, host traits, etc. also have a major influence on the efficiency of predator in managing prey population. Hence, functional response although an important tool, cannot alone be attributed to success and failure in biocontrol programs. However, the laboratory data provide information as to how these predators will respond to increasing prey density under simplified experimental conditions. For conclusive estimation of their biocontrol potential, further field based studies are needed.

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REFERENCES

Atlihan, R., Kaydan, M. B., Yarimbatman, A. and Okut, H. 2010. Functional response of the coccinellid predator *Adalia fasciatopunctata revelierei* to walnut aphid *Callaphis juglandis*. *Phytoparasitica*. **38:** 23-29.

Atwal, A.S. and Sethi, S.L. 1963. Biochemical basis for the food preference of a predator beetle. *Current Science*. **32:** 511-512.

Beddington, J.R., Hassel, M.P. and Lawton, J.H. 1976. The components of arthropod predation-II. The predator rate of increase. *Journal of Animal Ecology*. **45:** 165-185.

Dixon, A.F.G. 2000. *Insect Predator-Prey Dynamics; Ladybird Beetles and Biological Control*. Cambridge University Press. Cambridge. p. 275.

Dobzhansky, T. 1933. Geographical variation in ladybeetles. *American Naturalist*. **67:** 97-126. (doi:10.1086/280472)

Farhadi, R., Allahyari, H. and Juliano , S.A. 2010. Functional response of larval and adult stages of *Hippodamia variegata* (Coleoptera: Coccinellidae) to different densities of *Aphis fabae* (Hemiptera: Aphididae). *Environmental Entomology*. **39:** 1586-1592.

Franzmann, B.A. 2002. *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), a predacious ladybird new in Australia. *Australian J. of Entomolology*. **41:** 375-377.

Gordon, R.D. 1987. The first North American records of *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae). *J. of the New York Entomological Society*. **95:** 307-309.

Hodek, I. and Honek, A. 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers. Boston. p. 464.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*. **9:** 385-398.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Memoirs of Entomological Society of Canada*. **48:** 1-86.

Isikber, A.A. 2005. Functional response of two coccinellid predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, to the cotton aphid, *Aphis gossypii*. *Turk J. of Agri. Forestry*. **29:** 347-355.

Jafari, R. and Goldasteh, S. 2009. Functional response of *Hippodamia variegata* (Goeze) (Coleoptera: coccinellidae) on *Aphis fabae* (Scopoli) (Homoptera: aphididae) in laboratory conditions. *Acta Entomologica Serbica*. **14(1):** 93-100.

Jafari, R. and Shoushtari, R.V. 2010. Effect of different temperatures on life developmental stages of *Hippodamia variegata* Goeze (Col., Coccinellidae), feedingon *Aphis fabae*Scopoli (Hem., Aphididae). *J. of Entomological Research*. **1:** 289-297.

Jervis, M.A., Copland, M.J.W. and Harvey, J.A. 2005. The life cycle. In**:** I*nsects as Natural Enemies: A Practical Perspective,* M.A., Jervis (Ed). Springer, The Netherlands, pp 73-165.

Juliano, S.A. 2001. Non-linear curve fitting: Predation and functional response curves. In: *Design and Analysis of Ecological Experiments*, 2nd edition, S.M., Scheiner and J., Gurevitch, (Eds.). Chapman and Hall, New York, pp. 178-196.

Khan, A. A. 2009. Functional response of *Adalia tetraspilota* (Hope) (Coleoptera: Coccinellidae) on cabbage aphid, *Brevicoryne brassicae* (L.) (Homoptera: Aphididae). *J. Biol. Control.* **23:** 243-248.

Khan, A. A. and Mir, R. A. 2008. 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). *J. Biol. Control.* **22:** 291-298.

Khan, A. A., Mir, R. A. and Zaki, F. A. 2007. Relative abundance of predacious ladybird beetle (Coleoptera: Coccinellidae) in Kashmir. *J. Aphidology*. **21:** 23-30.

Khan, A. A., Zaki, F. A., Khan, Z. H. and Mir, R. A. 2009. Biodiversity of predacious ladybird beetles (Coleoptera: Coccinellidae) in Kashmir. *J. Biol. Control.* **23:** 43-47.

Khan, A.A. 2010. Stage-specific functional response of predaceous ladybird beetle, *Harmonia eucharis* (Mulsant) (Coleoptera: Coccinellidae) to green apple aphid, *Aphis pomi* De Geer (Hemiptera: Aphididae). *J. Biol. Control.* **24:** 222-226.

Kontodimas, D.C. and Stathas, G.J. 2005. Phenology, fecundity and life table parameters of the predator *Hippodamia variegata* reared on *Dysaphis crataegi. Biocontrol.* **50:** 223-233.

Lee, J.H. and Kang, T.J. 2004. Functional response of *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biological Control.* **31:** 306-310.

Meyer, J. S., Ingersoll, C. G., Mcdonald, L. L., and Boyce, M. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology*. **67:** 1156-1166.

Mills, N.J. 1982. Satiation and the functional response: A test of a new model. *Ecological Entomology*. **7:** 305-315.

Murdoch ,W.W. and Oaten, A. 1975. Predation and population stability. *Advances in Ecological Research*. **9:** 1-131.

Nakamura, K. 1977. A model for the functional response of a predator to varying prey densities; based on the feeding ecology of wolf spiders. *Bull. Nati. Inst. Agri. Sci. (Tokyo), Series C.* **31:** 29-89.

Pervez, A. and Omkar. 2005. Functional responses of coccinellid predators: An illustration of a logistic approach. *Journal of Insect Science*. **5:** 1-6.

Research Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.

Rana, J. S., Dixon, A. F. G. and Jarosik, V. 2002. Costs and benefits of prey specialisation in generalist insect predator. *Journal of Animal Ecology*. **71:** 15-22.

Rogers, D. 1972. Random search and insect population models. *J. Anim. Ecol.* **41:** 369–383.

Saleh, A., Ghabeish, I., Al-Zyoud, F. Ateyyat, M. and M. Swais. 2010. Functional response of the predator *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) feeding on the aphid *Brachycaudus helichrysi* (Kaltenbach) infesting chrysanthemum in the Laboratory. *Jordan J. Biol. Sciences*. **3:** 17-20.

Thompson, S.N. 1999. Nutrition and culture of entomophagous insects. *Annual Rev. Entomology*. **44:** 561-592.

Veeravel, R. and Baskaran, P. 1997. Functional and numerical responses of *Coccinella transversalis* Fab and *Cheilomenes sexmaculata* Fab.feeding on the melon aphid, *Aphis gossypii* Glov. *Insect Science Applications*. **17:** 335-339.

Wu, X., Zhou, X. and Pang, B. 2010. Influence of five host plants of *Aphis gossypii* Glover on some population parameters of *Hippodamia variegata* (Goeze) *J. Pest Science*. **83:** 77-83.