Functional Response of Larval and Adult Stages of *Hippodamia variegata* (Coleoptera: Coccinellidae) to Different Densities of *Aphis fabae* (Hemiptera: Aphididae)

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Environ. Entomol. 39(5): 1586–1592 (2010); DOI: 10.1603/EN09285

ABSTRACT We compare the efficiencies of different stages of *Hippodamia variegata* (Coleoptera: Coccinellidae) preying on *Aphis fabae* (Scolpoli) (Hemiptera: Aphididae) by estimating the functional responses of all stages. The experiments were carried out on leaf disks in petri dishes with 15–20 replicates. Our results revealed that all larval instars and adult males and females of *H. variegata* exhibited type II functional responses on different densities of prey. The rate of searching efficiency and handling time were estimated as 0.063 h^{-1} and 6.933 h for first instar, 0.059 h^{-1} and 3.343 h for second instar, 0.103 h^{-1} and 1.909 h for third instar, 0.114 h^{-1} and 0.455 h for fourth instar, 0.159 h^{-1} and 1.194 h for male, 0.093 h^{-1} and 0.409 h for female, respectively. Thus, handing time decreased from first instar to female. Handling times of males were significantly greater than those of females. The most effective stages of *H. variegata* were females, fourth instars, and males. The efficiency of females was nearly three times greater than that of males. The voracity of larval stages and male and female adults of *H. variegata* were estimated as 2.93, 5.85, 12.13, 45.13, 18.33, and 44.60 (aphids/d), respectively.

KEY WORDS functional response, *Hippodamia variegata*, *Aphis fabae*, searching efficiency, handling time

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Black bean aphid, *Aphis fabae* (Scolpoli) (Hemiptera: Aphididae), is a polyphagous species (Blackman and Eastop 2007) that feeds on almost 200 host plant species. *A. fabae* is a major pest on beans and sugar beets in Iran (Esmaili et al. 1993). It is a serious sap feeder and vector of viruses on sugar beets, transmitting >30 viruses, mainly in the nonpersistent group (Blackman and Eastop 2007). Aphid feeding results in a reduction of 7–33% of crude protein levels in bean leaf tissue (Shannag 2007).

The major natural enemies of *A. fabae* are predators, including the coccinellids *Hippodamia convergens* (Guérin-Méneville) (Coleoptera: Coccinellidae), *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), *Coccinella novemnotata* (Coleoptera: Coccinellidae) and *C. septempunctata* (L.) (Coleoptera: Coccinellidae), and the chrysopids *Chrysopa oculata* (Say) (Neuroptera: Chrysopidae) and *C. nigricornis* (Ehler et al. 1997; Aslan and Uygun 2005; Kunert et al. 2008). The palaearctic coccinellid species *H. variegata* is a widespread aphidophagous predator in Europe (Hodek and Honek 1996). *H. variegata* has been cited as the most important predator of aphids on pepper in Bulgaria, on maize in Ukraine, on shrubs in Italy, on grain in India, and on cotton in Turkmenistan (Kontodimas and Stathas 2005). It has been recorded feeding on 19 different aphid species in Turkey (Aslan and Uygun 2005) and on 12 different aphid species and a psyllid on a variety of crops, weeds, and ornamental plants in Australia (Franzmann 2002). *H. variegata* is the most abundant coccinellid species in Iran, and understanding factors that contribute to its success as a predator may be practically important for enhancing its impact on pest aphid populations.

One of the criteria for evaluating the efficiency of a predator is its feeding response to changes in prey density, or its functional response, defined as the number of prey that an individual predator kills as a function of prey density (Holling 1966). The functional response gives a quantitative description of the behavior of a predator when it encounters different densities of its prey.

Although *H. variegata* is a widespread coccinellid species, there is no detailed information about functional responses of its various life stages to aphids. To provide information on functional responses of different life stages of this species and to determine the relative efficiency of different stages of *H. variegata* as a biological control agent, functional responses of different stages of this ladybird to different densities of *A. fabae* were quantified in a laboratory setting.

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Materials and Methods

Insect Culture. *H. variegata* were collected from an alfalfa farm in Karaj region, Tehran province, Iran. The main stock colonies of *H. variegata* and *A. fabae* were reared in a controlled environmental chamber (25 ± 1°C, 70 ± 10% RH, and a photoperiod of 16:8 h L:D). Aphids were reared on living broad bean plants, *Faba vulgaris,* at 21 ± 1°C and 70 ± 10% RH, and a photoperiod of 16:8 h L:D. The broad bean plants were planted in pots that were filled with sawdust and fertilized with HORTI micro and macro elements fertilizer (2% solution in water) every 4 d.

Functional Response. After two generations, adult predators were transferred from the stock culture into plastic boxes (20 × 15 × 12 cm). Several pieces of crumpled paper were placed in each box to provide oviposition sites. The boxes were placed in an incubator at 23 ± 1°C and 70 ± 10% RH, and a photoperiod of 16:8 h L:D. To obtain eggs of uniform age, male and female pairs were transferred to petri dishes (9 cm) that were maintained in an incubator and checked at 6-h intervals. Using this procedure, different larval stages (first, second, third, and fourth instars) of predators that were similar in age (0–6 h old) were produced. Adults used in the experiment were 5-d-old mated males and females. Based on several preliminary tests on different stages, different densities of *A. fabae* of the same physiological ages (reared for 4–5 d at 21°C) were used: 2, 4, 6, 8, 10, and 15 aphids for first instars; 2, 4, 8, 12, 16, 22, and 28 aphids for second instars; 2, 4, 8, 16, 32, 45, and 65 aphids for third instars; 2, 4, 8, 16, 32, 64, 100, and 130 aphids for fourth instars; 2, 4, 8, 16, 32, 45, and 60 aphids for adult males; and 2, 4, 8, 16, 40, 60, 80, and 100 aphids for adult females. The experimental petri dishes were examined after 24 h to record the number of aphids consumed. For each stage-sex combination, experiments were replicated 15–20 times simultaneously. Greater replication was allocated to the lowest three densities to obtain more precise information about the initial part of functional response curve.

Data Analysis. Data analysis for functional responses includes two steps (Juliano 2001). In the first step, the shape (type) of functional response is determined. A logistic regression of proportion of eaten prey versus initial number of prey offered is the most effective way to make this determination (Juliano 2001). To do this, a polynomial logistic function was fitted to data:

$$Na/N_0 = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}{1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)} \qquad [1]$$

where P_0, P_1, P_2, and P_3 are the parameters to be estimated using the CATMOD procedure in SAS software (Juliano 2001, SAS Institute Inc. 2003). The six data sets were fitted individually to equation 1 and types of functional responses were determined by examining the signs of P_1 and P_2. A positive linear parameter (P_1) together with a negative quadratic parameter (P_2) would indicate a type III functional response, whereas if the linear parameter is negative, a type II functional response is indicated (Juliano 2001). In the second step, nonlinear least squares regression (PROC NLIN; SAS Institute Inc. 2003) was used to fit Rogers' type II random predator equation (Rogers 1972) to data and to estimate the functional responses parameters. Because prey were depleted during the experiment, this model, which does not assume constant prey density, is appropriate for this experiment (Rogers 1972, Juliano 2001). Holling's disc equation, in contrast, is based on an assumption of unchanging prey density (Rogers 1972), and is thus inappropriate for this experiment (Juliano 2001). The form of Rogers' type II random predator model is:

$$N_a = N_0\{1 - \exp[-a(T - T_hN_a)]\} \qquad [2]$$

where N_0 is initial prey density, N_a, number of prey consumed, T is the total time (24 h), a is the attack rate (h^{-1}), and T_h is handling time in hours. Pairwise comparisons of parameters of functional responses for all possible pairs of fourth instars, males, and females were performed using the indicator variable method (Juliano 2001) as follows:

$$N_a = N_0\{1 - \exp[-(a + D_a(j))(T - (T_h + D_{Th}(j))N_a)]\} \qquad [3]$$

where j is an indicator variable that takes on a value of 0 for the first data set and one for the second data set. The parameters D_a and D_{Th} estimate the differences between the data sets being compared for the values of the parameters a and T_h, respectively. In other words, the attack rate for one stage is a, and that for another stage is $a + D_a$. Testing for a significant difference in searching efficiencies between two stages is accomplished by testing the null hypothesis that $D_a = 0$ (Juliano 2001, Allahyari et al. 2004).

Voracity of fourth instars, males, and females of *H. variegata* on *A. fabae* was determined according to the following equation (Cabral et al. 2006, Moura et al. 2006):

$$V_o = (A - a_{24})ra_{24} \qquad [4]$$

where V_o is the quantification of voracity, A is number of prey available, a_{24} is number of prey alive after 24 h, and ra_{24} is the ratio of prey found alive after 24 h in a control treatment without a predator (i.e., number of aphids alive after 24 h/initial number of aphids). Analysis of variance (ANOVA) was performed to test differences in voracity at maximum densities of *A. fabae* for different stages of the predator (first instar: 15 aphids; second instar: 28 aphids; third instar: 65 aphids; fourth instar: 130 aphids; adult male: 60 aphids; adult female: 100 aphids). Following significant ANOVA, a Ryan-Einot-Gabriel-Welsch Multiple Range test (SAS Institute Inc. 2003) was used for pairwise comparisons of means.

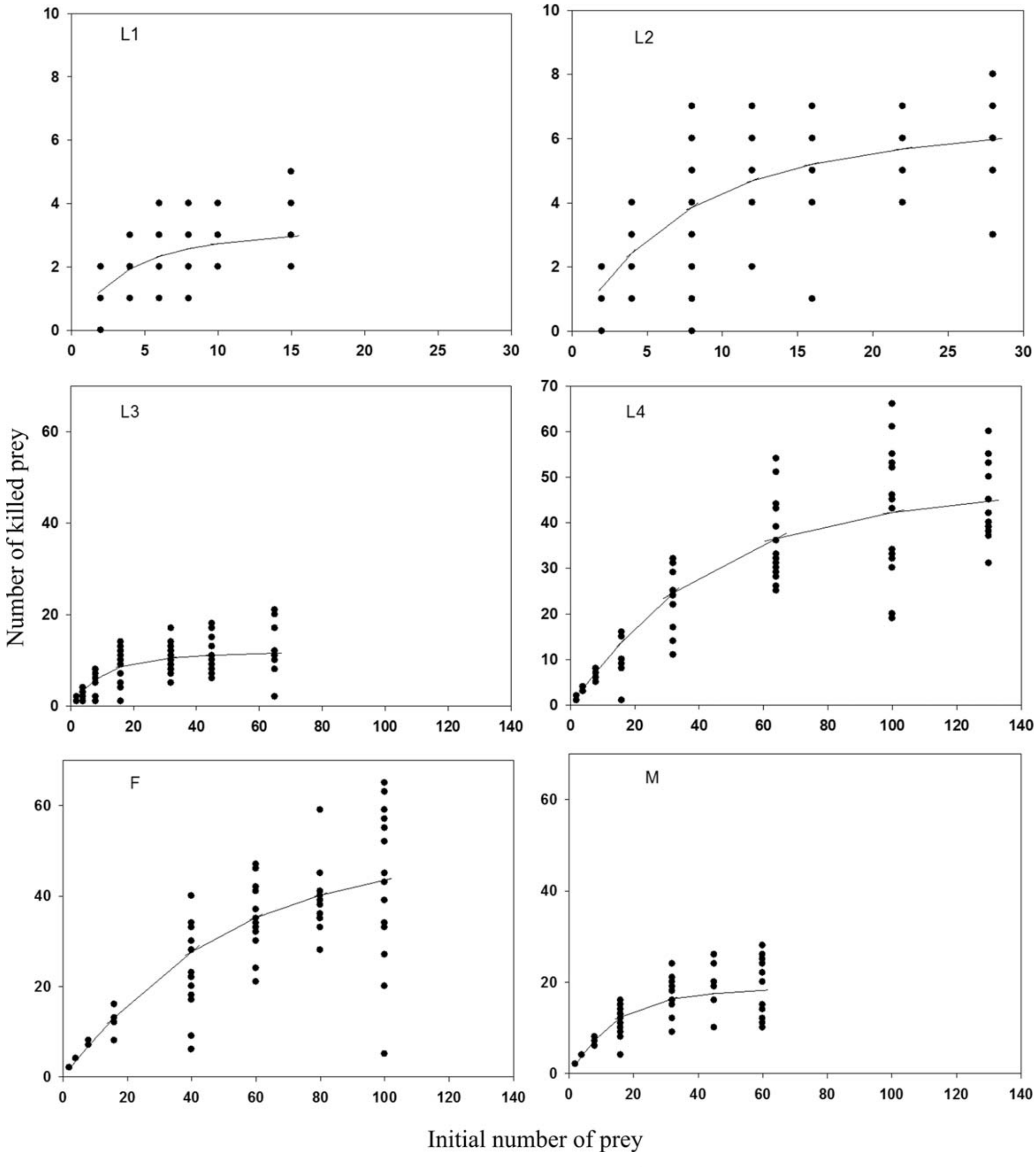

Fig. 1. Functional response of *H. variegata* on different densities of *A. fabae*: (L1) first larval instar, (L2) second larval instar, (L3) third larval instar, (L4) fourth larval instar, (M) male, and (F) female. Symbols are observed data and lines were predicted by model (equation 2).

Results

In all experiments, the number of consumed prey increased with increasing the prey densities (Fig. 1). Fitting the polynomial logistic regression (equation 1) to data sets demonstrated that all developmental stages of *H. variegata* showed a type II functional response to *A. fabae* (Table 1). In all cases, the linear term of the polynomial regression of the proportion of aphids consumed versus initial density was negative. The functional responses for *H. variegata* preying on *A. fabae* over a 24-h period were therefore fitted to Rogers' random predator equation (equation 2). Maximum predation rate increased as *H. variegata* developed from one life stage to another (Fig. 1). Estimates of attack rate (a) were greatest for adult males and fourth instar larvae, followed by third instar larvae (Table 2). Handling times of adult females and fourth instar larvae were 0.4098 and 0.4547 h, respectively, and were substantially shorter than the handling times of other stages

Table 1. **Results of logistic regression analysis of the proportion of *A. fabae* eaten by different stages of *H. variegata* against initial no. of aphids offered**

Instars	Coefficient	Estimate	SE	Chi-squared value	*P* value
First instar	Constant	1.2282	0.8561	2.06	0.1514
	Linear	−0.4227	0.3814	1.23	0.2677
	Quadratic	0.0284	0.0493	0.33	0.5645
	Cubic	−0.0008	0.00186	0.18	0.6681
Second instar	Constant	1.9371	0.4327	20.04	<0.0001
	Linear	−0.3871	0.1045	13.27	0.0002
	Quadratic	0.0191	0.0073	6.88	0.0084
	Cubic	−0.00034	0.00015	5.14	0.0233
Third instar	Constant	2.472	0.3024	66.85	<0.0001
	Linear	−0.1912	0.0358	28.53	<0.0001
	Quadratic	0.0035	0.00131	9.62	0.0019
	Cubic	−0.00002	0.00001	5.22	0.0223
Fourth instar	Constant	3.0128	0.2375	160.95	<0.0001
	Linear	−0.0702	0.0120	34.27	<0.0001
	Quadratic	0.0005	0.00017	8.57	0.0034
	Cubic	−0.45E-6	7.525E-7	3.70	0.0544
Male adult	Constant	5.6062	0.6020	86.71	<0.0001
	Linear	−0.3808	0.0601	40.09	<0.0001
	Quadratic	0.00835	0.00178	22.01	<0.0001
	Cubic	−0.0001	0.00002	15.92	<0.0001
Female adult	Constant	5.3553	0.4786	125.18	<0.0001
	Linear	−0.1977	0.0255	59.95	<0.0001
	Quadratic	0.0025	0.00043	34.81	<0.0001
	Cubic	−0.00001	2.242E-6	24.76	<0.0001

(Table 2). Comparisons of attack rates and handling times for fourth instar larvae, adult males, and adult females yielded no significant pairwise differences in attack rate (Table 3), but handling times for males were significantly longer than those for either adult females or fourth instar larvae (Table 3). Handling times for adult females and fourth in stars did not differ (Table 3).

Voracity. Voracity of different life stages of *H. variegata* at maximum densities of *A. fabae* during 24 h period was significantly different among different life stages (F (5, 88) = 64.67; $P < 0.0001$). In general, voracity increased with instar, and adult females had greater voracity than did adult males (Table 4). There was no significant difference between fourth instar larvae and adult females, and these two groups had the highest voracity, significantly greater than those of all other life stages (Table 4). Among remaining life stages, males had voracity significantly greater than those for first or second instar larvae (Table 4). Voracity was lowest for first, second, and third instar larvae, with the only significant difference among these three life stages occurring between first instars and third instars (Table 4).

Table 2. **Estimated parameters for the random predator equation (Rogers 1972) for *H. variegata* feed on *A. fabae***

Stage	Parameter	Estimate	Asymptotic SE	Asymptotic 95% CI	
				Lower	Upper
First instar	a	0.0634	0.0164	0.0309	0.0959
	T_h	6.9332	0.6657	5.6117	8.2547
Second instar	a	0.0596	0.0103	0.0392	0.0799
	T_h	3.3433	0.2400	2.8677	3.8189
Third instar	a	0.1031	0.0293	0.0451	0.1612
	T_h	1.9099	0.1272	1.6579	2.1619
Fourth instar	a	0.1138	0.0223	0.0697	0.1578
	T_h	0.4547	0.0280	0.3993	0.5100
Adult males	a	0.1589	0.0435	0.0728	0.2451
	T_h	1.1945	0.0691	1.0577	1.3312
Adult females	a	0.0926	0.0212	0.0507	0.1346
	T_h	0.4098	0.0480	0.3149	0.5048

a, attack coefficient; T_h, handling time.

Table 3. **Parameters estimated by an equation with indicator variable for comparing functional response parameters of female, male and fourth instar larva of *H. variegata***

Parameter	Estimate	Asymptotic SE	Asymptotic 95% CI	
			Upper	Lower
Female-male				
0.1683	−0.0425	0.0479	0.0629	D_a
0.9582	**0.6042**	**0.0804**	**0.7812**	D_{Th}
Female-fourth instar				
0.0170	−0.0610	0.0179	−0.0220	D_a
0.0212	−0.1148	0.0312	−0.0468	D_{Th}
Male-fourth instar				
0.1149	−0.0375	0.0356	0.0409	D_a
0.8619	**0.6070**	**0.0579**	**0.7344**	D_{Th}

Significant difference parameters shown in bold face.

Discussion

Reproduction of aphids during experiments can be a major challenge to investigations of predation rates on aphids. Reproduction changes the number of aphids, rendering it impossible to determine how many newly produced nymphs have been eaten. We used 4- to 5-d-old aphids reared at a controlled temperature. Preliminary data showed that surviving aphids produce their first nymphs 12–24 h after our 24-h test period. Thus, we used aphids that were similar in size to adults, but unlikely to produce nymphs.

Our estimates of maximum numbers of aphids attacked per day were 52.78 for fourth instars, 58.56 for females, and 20.1 for males. Thus killing efficiency of adult females may be as much as 2.9 times that of adult males. There is no significant difference between handling times of females and fourth instar larvae, but there is significant difference between handling times of females and males (Table 4). This suggests that the greater killing efficiency of females compared with males arises because of differences in handling time. Our observation that the fourth instar of *H. variegata* was the stage that consumed the greatest proportion of *A. fabae* over 24 h is consistent with observations on other coccinellids indicating that fourth instars consumed over 60% of total prey consumption by all larval stages (Hodek and Honek 1996, Lee and Kang 2004).

H. variegata displayed a type II functional response on *A. fabae* in all developmental stages. This type of functional response has been reported for many different coccinellids, including: *Aphidecta obliterata* (L.) and *Adalia bipunctata* (L.) preying on *Elatobium abietinum* (Walker) (Timms et al. 2008), larvae and adults of *Propylea quatuordecim-*

Table 4. Voracity (mean ± SE) of different stages of *H. variegata* stages at max *A. fabae* densities (first instar: 15 aphids; second instar: 28; third instar: 65; fourth instar: 130; male adult: 60; female adult: 100) at 23°C

Stage	First instar	Second instar	Third instar	Fourth instar	Male adult	Female adult
Estimate	2.93 ± 0.3d	5.85 ± 0.32cd	12.13 ± 1.45bc	45.13 ± 2.1a	18.33 ± 1.66b	44.6 ± 4.77a

Means for each developmental instars followed by the same letters are not statistically different (Ryan-Einot-Gabriel-Welsch Multiple Range test, $P < 0.05$).

punctata preying on *Diuraphis noxia* (Mordvilko) (Messina and Hanks 1998), *Coccinella undecimpunctata* (L.) preying on *A. fabae* and *Aleyrodes proletella* (Moura et al. 2006), male adults of *Cheilomenes sulfurea* preying on *A. fabae* (Hodek et al. 1984), adult females of *Cheilomenes sexmaxulata, Propylea dissecta,* and *Coccinella transversalis* preying on *Aphis craccivora* (Koch) or *Myzus persicae* (Sulzer) (Pervez and Omkar 2005), and adults of *Curinus coeruleu* preying on *Heteropsylla cubana* (Silva et al. 1992). In contrast, type III functional responses appear to be relatively rare among coccinellids. Içsikber (2005) determined functional responses of two coccinellids species under three temperature regimes, and found that only *Cycloneda sanguinea* exhibited a type III functional response, and only at 25°C. Sarmento et al. (2007) showed that *Eriopis connexa* exhibits different types of functional responses to *Macrosiphum euphorbiae* (type III) and *Tetranychus evansi* (type II).

Holling (1959) identified three types of functional responses of predators and parasitoids. Among them, only type III produces density-dependence mortality (Murdoch and Oaten 1975). Nicholson (1933) stated that density-dependent mortality factors could regulate the population and Holling (1965) postulated that stable equilibrium densities and damping of population oscillations would be more likely with type III rather than type II functional responses. Other investigators have similarly postulated that a predator with a type III functional response could contribute more to regulation of prey density than a predator with a type II functional response (Murdoch 1969, Murdoch and Oaten 1975). One postulated mechanism for type III functional responses is concentration of predator hunting effort in high-density patches (Hertlein and Thorarinsson 1987). In principle, this mechanism could, have operated in our experiment; however, we found no evidence of type III functional response by *H. variegata,* suggesting that this mechanism is not likely for this predator-prey system. Our experiment would not have detected type III functional responses produced by other mechanisms. In a multiple prey system, generalist predators may show switching behavior (Murdoch 1969), which has been suggested as a mechanism generating type III functional responses (e.g., Holling 1966, Murdoch and Oaten 1975). Another postulated mechanism producing type III functional responses is predator learning, wherein predator success increases with density as individual predators learn to hunt more effectively when prey are abundant (Holling 1965, Murdoch and Oaten 1975). Our experiment was a short-term, single-prey species test, hence these two postulated mechanisms for type III functional responses could not have acted in our experiment. Thus, we cannot rule out type III functional responses for *H. variegata* under other circumstances (i.e., multiple prey types, longer term trials). Though type III functional responses can contribute to stabilizing prey populations at low levels (i.e., the goal of biological control), they are often not sufficient to do so (Hassell 1978, Luck et al., 1979) in part because type III functional responses yield inverse-density-dependent mortality at high prey densities.

The success of coccinellids in biological control (Obrycki and Kring 1998) coupled with the prevalence of type II functional responses (previous paragraph) suggests that successful biological control is possible with type II functional responses. Fernández-Arhex and Corley (2003) reviewed the literature on functional responses of parasitoids used in biological control and showed that only about a quarter of studies showed type III functional responses, providing further evidence that although functional responses are a one element in selection of efficient biocontrol agents, there is no general relationship between success in biocontrol and the type of functional response. Other aspects of prey and predator biology, including: prey preference, switching, intrinsic rate of increase of prey and predator, killing rate of predator, host patchiness, predator patch allocation time, effect of host plant, effect of abiotic factors, and intra- and interspecific predator competition, can all have important effects on the efficiency of a biocontrol agent (Murdoch et al. 1985, Murdoch and Briggs 1996, Obrycki and Kring 1998).

Functional response experiments are routinely done in controlled conditions, like those used in our experiments. Clearly, in nature, the predator will encounter uncontrolled and highly variable conditions. Changes in temperature, humidity, and other aspects of weather could radically change the functional responses of predators to change in prey density. It is difficult to predict a priori, whether such climatic effects will increase or decrease the number of killed prey at each density.

One practical conclusion of this study is that females and fourth larval instar are the stages of *H. variegata* that are most effective as predators. Because efficiency of females was nearly three times greater than that of males, it might be advantageous for biological control to release populations with high female:male ratios. This, however may be impractical because of constraints on sorting individuals for mass release. Another practical implication of our results arises because adults and late instar larvae are much more efficient than are early instar larvae. This result suggests that mass releases of this predator may be most effective if relatively synchronous populations can be reared and released primarily as late-stage individuals (fourth instars, adults). Such releases would facilitate rapid killing of aphid prey immediately after release.

Acknowledgments

This research project was funded in part by the Center of Excellence in Biological Control, Ministry of Science, Research, and Technology, Iran.

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Received 2 October 2009; accepted 23 June 2010.