JOURNAL OF ENTOMOLOGICAL
SOCIETY OF IRAN
2013, 33(2): 33-43

Larval age-specific searching efficiency of *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae) preying on different densities of *Aphis craccivora* (Hem.: Aphididae)

Kh. Madahi, A. Sahragard[*] and R. Hosseini
Department of Plant Protection, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran
*Corresponding author, E-mail: sahragard@guilan.ac.ir

Abstract

Searching efficiency (*a′*) (attack rate) and handling time are two major components of natural enemies' functional response and are usually used to evaluate their effectiveness. The age-specific searching efficiency of *Aphidoletes aphidimyza* (Rondani) was studied during its larval stage. The experiment was conducted in terms of age-specific functional response to the varying density (5, 10, 20, 40, 60 and 80) of third instar nymphs of *Aphis craccivora* (Koch) at 23 ± 1 °C, 70 ± 5% R.H. and a photoperiod of 16: 8 h (L: D). Parameter estimates for logistic regressions showed a type III functional response at all larval ages to the varying density of *A. craccivora*. The age-specific handling times (T_h) were estimated using Rogers random-attack equation, varied with the age of larval predator. The searching efficiency showed a similar and increasing trend at all predator larval ages. The estimated maximum rates of predation (T / T_h) for the total larval stage were inversely related to prey density. It was concluded that *A. aphidimyza*, with type III functional response in all its larval stage, could be considered as a highly effective biological agent in suppressing and regulating *A. craccivora* population.

Keywords: Age-specific searching efficiency, prey density, predator larval stage

چکیده

قدرت جستجوی وابسته به عمر در دوره‌ی لاروی مگس *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae) با شکار از تراکم‌های مختلف شته‌ی *Aphis craccivora* (Hem.: Aphididae)

خدیجه مداحی، احد صحراگرد و رضا حسینی

قدرت جستجو (*a′*) یا نرخ حمله و زمان دست‌یابی دو جزء مهم واکنش تابعی دشمنان طبیعی هستند و به‌طور معمول برای ارزیابی کارایی آن‌ها استفاده می‌شوند. قدرت جستجوی وابسته به عمر مگس *Aphidoletes aphidimyza* (Rondani) در دوره‌ی لاروی آن مورد مطالعه قرارگرفت. آزمایش براساس واکنش تابعی وابسته به عمر نسبت به تراکم‌های مختلف (۵، ۱۰، ۲۰، ٤٠، ٦٠ و ۸۰) پوره‌های سن سوم *Aphis craccivora* (Koch) در شرایط ۱ ± ۲۳ درجه‌ی سلسیوس، ۵ ± ۷۰ درصد رطوبت نسبی و دوره‌ی نوری ۸ :۱٦ ساعت تاریکی: روشنایی انجام شد. برآورد پارامترها با استفاده از رگرسیون لجستیک، واکنش تابعی نوع سوم را برای کل دوره‌ی لاروی شکارگر نسبت به تراکم‌های متفاوت *A. craccivora* نشان داد. زمان دست‌یابی (T_h) وابسته به سن برآوردشده با استفاده از معادله‌ی نرخ حمله‌ی تصادفی Rogers با عمر لاروی شکارگر تغییر کرد. قدرت جستجو با پیشرفت دوره‌ی لاروی دارای روند مشابه و افزایشی بود. حداکثر نرخ شکارگری (T / T_h) برای مجموع دوره‌ی لاروی وابسته به عکس تراکم طعمه بود. نتیجه‌گیری شد که *A. aphidimyza* با دارا بودن واکنش تابعی نوع سوم در تمام دوره‌ی لاروی خود می‌تواند به‌عنوان عامل کنترل بیولوژیک بسیار مؤثر در کاهش و تنظیم جمعیت *A. craccivora* در نظر گرفته شود.

واژگان کلیدی: قدرت جستجوی وابسته به سن، تراکم شکار، مرحله‌ی لاروی شکارگر

Introduction

The cowpea aphid, *Aphis craccivora* (Koch) as a cosmopolitan pest feeds on several host plants. It is considered as a major pest of important economic crops such as alfalfa, *Medicago sativa* L., beans (Fabaceae) and cowpea, *Vigna unguiculata* (L.), in Africa, Asia and Latin America (Singh & Jackai, 1985; Pettersson *et al*., 1998). It has been reported that this aphid can transmit some plant pathogenic viruses (Coceano *et al*., 1989; Chen *et al*., 1999).

The aphidophagous cecidomyiid, *Aphidoletes aphidimyza* (Rondani) is an effective predator of many aphid species worldwide in glasshouses, on field crops, and fruit trees (Morse, 1981). Since 1973, it has been used for the biological control of aphid populations in greenhouses (Asyakin, 1973; Markkula *et al*., 1979; Kulp *et al*., 1989). It shows great promise as a biological control agent because of its high degree of density dependency (El-Titi, 1973), its tendency to kill more aphids than it consumes (Uygun, 1971), and its compatibility with many pesticides (Warner & Croft, 1982).

In recent years, intensive use of different chemical pesticides cause negative effects on the environment. Therefore, using natural enemies in the biological control of insect pests become an important component of integrated pest management (Hodek & Honek, 1996; Atlihan & Bora Kaydan, 2010). In order to enhance or augment the effect of natural enemies in a prey population, it is necessary to understand the interaction components between natural enemies and prey (Rabb, 1974). Prior to the use of natural enemies in a biological control program, it is important to measure the effectiveness of natural enemies (Bazzocchi & Burgio, 2001). Functional response is an aspect of foraging behaviour of natural enemies that evaluates their efficacies (Trexler *et al*., 1988; De Clercq *et al*., 2000; Reis *et al*., 2003, 2007; Badii *et al*., 2004; Fathipour *et al*., 2006; Timms *et al*., 2008). Functional response is also a behavioural characteristic that reveals different features of prey-predator interactions (Lester & Harmsen, 2002) and shows the change in the predation rate with changing prey density (Solomon, 1949).

When the number of prey eaten is plotted against prey density, it can follow one of three mathematical models: type I (linear), type II (convex) or type III (sigmoid) (Pervez & Omkar, 2005). In the type I model, the proportion of prey eaten increases linearly with prey availability up to a maximum. In the type II model, the proportion of prey attacked declines monotonically with prey availability. The type III model shows a sigmoid relationship in which the proportion of prey consumed is positively density-dependent over some region of prey density. (Holling, 1966; Trexler *et al*., 1988; De Clercq *et al*., 2000; Timms *et al*., 2008). Several other types of functional responses have been reported, such as type IV (Luck 1985) and type V (Sabelis, 1992).

Functional response manifests two significant parameters: (1) attack rate or searching efficiency (a') and (2) handling time (T_h). They are usually used to evaluate the effectiveness of predators and parasitoids (Hassel & Waage, 1984). The rate of these parameters are affected by different factors such as: age of predator (Ding-Xu *et al*., 2007) and parasitoid (Sahragard, 1989; Asadi *et al*., 2012), developmental stages of predator (Yaşar & Özger, 2005a; Farhadi *et al*., 2010), sex of predator (Rocha & Redaelli, 2004; Farhadi *et al*., 2010), predator aggregation (Pervez & Omkar, 2005), parasitoid density (Tahriri *et al*., 2007), prey developmental stages (Taleb & Sardar, 2007), prey size (Cogni, 2002), prey availability and density (Laing & Osborn, 1974; Pervez & Omkar, 2005; Varone *et al*., 2007), host age and density (Chen *et al*., 2006; Chong & Oetting, 2006b), host developmental stages (De Jong & van Alphen, 1989; Godfray, 1994; Joyce *et al*., 2001; González-Hernández *et al*., 2005; Chong & Oetting, 2006a), host plant and plant architecture (De Clercq *et al*., 2000; Garcia & O'Neil, 2000; Madadi *et al*., 2007; Timms *et al*., 2008), temperature (Cave & Gaylor, 1989; Parajulee *et al*., 2006; Shojaei *et al*., 2006; Zamani *et al*., 2006; Ding-Xu *et al*., 2007; Atlihan & Chi, 2008), size of arenas (Yaşar & Özger, 2005b; Sabaghi *et al*., 2011b) and sublethal concentrations of insecticides (Rafiee Dastjerdi *et al*., 2009).

The functional response of *A. aphidimyza* has only been studied at its third larval instar to the varying density of *Aphis pomi* (Degeer) in a 24 h. experiment that was a type II (Morse & Croft, 1987). The objectives of the current study were to evaluate the searching efficiency of *A. aphidimyza* larvae in terms of functional responses during its larval stage to the different densities of *A. craccivora* as prey.

Materials and methods

Prey and predator stocks

The nymphs of *A. craccivora* were collected from black locust, *Robinia pseudoacacia* (L.), and reared on black-eyed bean, *V. unguiculata*. Larvae of *A. aphidimyza* were collected from the colony of *A. craccivora* in an infested black-eyed bean field at the Faculty of Agricultural Sciences, University of Guilan (North of Iran). The predators were reared for one generation on different instars of *A. craccivora* before starting the functional response experiments. All aphids and predator stocks were kept in a growth chamber at 23 ± 1 °C, 70 ± 5% relative humidity (R.H.), and a photoperiod of 16: 8 (L: D) h.

Functional response

In order to evaluate the searching efficiency and handling time of *A. aphidimyza* at its larval ages, the functional response of this predator to the different densities of third instar nymphs of *A. craccivora* as prey was studied at 23 ± 1 °C, 70 ± 5% R.H., and a photoperiod of 16: 8 (L: D) h. Since it was very difficult to separate larval instars of the predator, we used 'larval age' instead of larval instars. However, the experiments were started with first instar larvae of *A. aphidimyza* after egg hatch. They were daily exposed to the different densities (5, 10, 20, 40, 60 and 80) of third instar nymphs of *A. craccivora* separately on a black-eyed bean leaf in a transparent plastic container (15 × 13 × 3 cm). Aphids were gently transferred with a fine brush from the host plant to the leaves in experimental arenas. After 24 h, the number of aphids eaten by the larva was recorded. This was continued to the end of the larval stage. For each prey density, the experiment was replicated 20 times.

Data analysis

The type of the functional response was determined by logistic regression analysis [SAS/STAT, CATMOD procedure (SAS, version 9.1)] of the proportion of prey killed (N_e) in relation to initial prey density (N_0) (Trexler & Travis, 1993). The data were fitted to the logistic regression that describes the relationship between N_a / N_0 and N_0 (Juliano, 1993):

$$N_a / N_0 = \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3) / [1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)]$$

where P_0, P_1, P_2, and P_3 are the intercept of linear, quadratic and cubic coefficients, respectively, and estimated using the method of maximum likelihood. If the linear parameter P_1 is negative, a type II functional response is evident, whereas a positive linear parameter indicates density-dependent predation and thus a type III functional response (Juliano, 1993). Once, the type of functional response was determined, the model suggested for a type III response by Hassell *et al*. (1977) was used as follows:

$$N_a = N_0 [1 - \exp((d + bN_0)(T_hN_a - T) / (1 + cN_0))]$$

where b, c, and d are constants from the function that relate a' and N_0 in type III functional response:

$$a' = (d + bN_0) / (1 + cN_0)$$

Since results of nonlinear least square regression indicated that parameters c and d were not significantly different from zero; therefore we used a simple model of $a' = bN_0$ to estimate searching efficiency. Statistical analysis of the functional response was performed using the SAS software (SAS Institute, 2001). A nonlinear regression was used (the least-square technique with DUD initialization) to estimate parameters. Curves were drawn using the Excel software.

Results

The prey consumption rate at varying prey density in the larval developmental time of *A. aphidimyza* at the different larval ages (with type III functional response) was all significantly different (e.g., day 3; $F = 36713.9$; df = 2, 118; $P < 0.0001$). Parameter estimates for logistic regressions of proportion of prey killed (N_a / N_0) against number of prey offered (N_0) for *A. aphidimyza* during its larval period are presented in table 1. The larvae of *A. aphidimyza* showed a type III functional response at different larval ages to the varying densities of third instar nymphs of *A. craccivora* (fig. 1).

The estimated larval age-specific handling times (T_h), varied with the larval ages of the predator (table 2). The searching efficiency had similar and increasing trends as the predator larval stage developed (fig. 2). The estimated maximum rates of predation (T / T_h) for the total larval stage decreased as larval age increased, with no significant difference ($F = 3.167$; df = 1, 4; $P = 0.149$) (fig. 3).

Discussion

The functional response of a natural enemy offers a good framework to understand the success or failure of the predator in biological control programs (Waage & Greathead, 1988). Many studies have been devoted to the functional response of insect predators (e.g., Sarmento *et al.*, 2007; Seko & Miura, 2008; Xiao & Fadamiro, 2010; Sabaghi *et al.*, 2011a; Heidarian, 2012), but age-specific functional response in larval stage have received little attention. The current study is the first one on the functional response of *A. aphidimyza* during its larval age to the varying densities of third instar nymphs of *A. craccivora* as prey. This study showed that the age-specific functional response of *A. aphidimyza* at all larval ages was a type III response. It seems that total larval stage (i.e., this study) or lifetime functional response studies provide us with better insights into the behaviour of insect natural enemies. Predators which exhibit the type III functional response are commonly regarded as efficient biological control agents (Fernández-Arhex & Corley, 2003; Pervez & Omkar, 2005). Therefore, *A. aphidimyza*, which showed a type III response in all ages of its larval stage, can be considered as an effective biocontrol agent in regulating aphid populations, especially *A. craccivora*. However, many predators that have been successfully released as biological control agents, have exhibited a type II functional response on their prey (Ryoo, 1986; De Clercq *et al.*, 2000; Reis *et al.*, 2003; Badii *et al.*, 2004; Timms *et al.*, 2008).

Table 1. Maximum likelihood estimates from the logistic regression of the proportion of third instar nymphs of *Aphis craccivora* eaten as a function of initial prey densities by *Aphidoletes aphidimyza* larvae.

L. s. (d.)	**Parameters**	**Estimate**	**SE**	***P***
1	Constant	0.0262	0.1362	0.8476
	Linear	0.0225	0.00617	0.0003
	Quadratic	-0.00030	0.000062	0.0001
	Cubic	-5.18E-6	3.522E-6	0.1415
2	Constant	0.0728	0.2282	0.7498
	Linear	0.0589	0.0210	0.0050
	Quadratic	-0.00118	0.000516	0.0222
	Cubic	0.000005345	0.00000364	0.1427
3	Constant	0.9088	0.2398	0.0002
	Linear	0.00112	0.0214	0.9581
	Quadratic	-0.00021	0.000521	0.6932
	Cubic	4.693E-7	3.663E-6	0.8981
4	Constant	0.9090	0.2486	0.0003
	Linear	0.0357	0.0221	0.1063
	Quadratic	-0.00130	0.000535	0.0148
	Cubic	8.63E-6	3.752E-6	0.0214
5	Constant	0.5101	0.2617	0.0512
	Linear	0.00686	0.0270	0.7995
	Quadratic	-0.00009	0.000728	0.8980
	Cubic	-7.92E-7	5.514E-6	0.8858
6	Constant	0.8756	0.4072	0.0315
	Linear	0.0111	0.0455	0.8080
	Quadratic	-0.00113	0.00126	0.3661
	Cubic	9.605E-6	9.66E-6	0.3203

L. s. (d.) = Larval stage (days).

The attack rate or searching efficiency (a') and handling time (T_h) are the two major components of functional response that are usually used to evaluate the effectiveness of natural enemies (Hassel & Waage, 1984). The handling time was variable with a tendency to increase with age and its lowest and highest values were observed at the fifth and sixth day of larval age, respectively. However, the aim of this study was to determine the searching efficiency of *A. aphidimyza* during its larval stage. It had similar increasing trends at different larval ages. Similar studies have also shown this kind of relationship in other predators. Cédola *et al.* (2001) found that the searching efficiency (a') of *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae), preying on *Tetranychus urticae* (Koch), varied with the developmental stages of the predator, so that it was lower for protonymphs and adults than for deutonymphs. Yaşar & Özger (2005b) stated that the searching efficiency of *Oenopia conglobata* (L.) (Col.: Coccinellidae) at varying stages on *Hyalopterus pruni* (Geoffroy) (Hem.: Aphididae) was significantly different. The search rate decreased as stages developed, so that the searching efficiency of adults was shorter than all larval stages. Seko & Miura (2008) noted that the searching efficiency of *Harmonia axyridis* (Pallas) (Col.: Coccinellidae) on *Myzus persicae* (Sulzer) (Hem.: Aphididae) varied at different stages and it was the highest at the fourth instar larvae, followed by adult female, adult male, and third, second, and first instar larvae. Lee & Kang (2004) also found that the predation efficiency of this predator on *A. gossypii* increased as its stages developed. The searching efficiency was the highest in the third and fourth instars, followed by female adults. However, the study on *Scymnus subvillosus* (Goeze) (Col.: Coccinellidae), feeding on *H. pruni*, indicated that the searching efficiency was not affected by changes in the predator stage (Atlihan & Güldal, 2009). The searching efficiency of *Cryptolaemus montrouzieri* (Mulsant) was positively related to the number of mealy bug, *Planococcus citri* (Risso) (Hem.: Pseudococcidae) and different sizes of *Coleus blumei* (Bentham) (Labiatae) plants (Garcia & O'Neil, 2000).

Table 2. Constant coefficient (*b*) and the handling time (T_h) (h) of *Aphidoletes aphidimyza* in different larval ages fed on third instar nymphs of *Aphis craccivora*.

L. s. (d.)	P.	Estimate	SE	95% CI	
				Lower	Upper
1	*b*	0.00250	0.000345	0.00182	0.00318
	T_h	0.55000	0.025300	0.49990	0.60020
2	*b*	0.00392	0.000531	0.00287	0.00498
	T_h	0.54510	0.018900	0.50770	0.58240
3	*b*	0.00374	0.000375	0.00300	0.00448
	T_h	0.57390	0.014700	0.54480	0.60300
4	*b*	0.00518	0.000671	0.00385	0.00651
	T_h	0.63080	0.016500	0.59810	0.66360
5	*b*	0.00316	0.000336	0.00249	0.00383
	T_h	0.54030	0.026600	0.48720	0.59340
6	*b*	0.00643	0.001180	0.00402	0.00884
	T_h	0.93800	0.065600	0.80370	1.07240

L. s. (d.) = Larval stage (days); P. = Parameter.

Aging has been taken into account as a declining change from maturity to senescence (Rothstein, 1982). It has widely been studied in insects; however, previous studies have mainly focused on the effects of maternal and paternal age, age-specific fecundity, and foraging behaviour (Ponsonby & Copland, 1998; Dixon & Agarwala, 2002; Priest *et al*., 2002; Srivastava & Omkar, 2004). So far, few researchers have studied the effects of ageing on the type of functional response of predatory insects. Ambrose *et al*. (1996) reported a linear relationship between the age of *Rhynocoris marginatus* (Fabricius) (Hem.: Reduviidae) and the number of prey killed. Ding-Xu *et al*. (2007) found that the type of functional response by *Scolothrips takahashii* (Priesner) (Thys.: Thripidae) on the eggs of *Tetranychus viennensis* (Zacher) (Acari: Tetranychidae) was adversely affected by ageing. Females with the age of 3-18 days and males with the age of 3-6 days exhibited type II functional responses, while males with the age of 9 days or more had the type I functional response. It was also showed that the magnitude of the functional response in *S. takahashii* to the densities of *T. viennensis* decreased with increasing age. They concluded that the searching efficiency declined as the predator aged. It has recently been found that the length of the foraging period alters both the shape of the functional response and the magnitude of searching efficiencies, compared to a daily functional response proportional to the time spent foraging, as is classically done (Casas & McCauley, 2012).

It can be concluded that *A. aphidimyza*, with the type III functional response in all its larval age, could be considered as a highly effective biological agent in suppressing and regulating aphid species populations, especially *A. craccivora*.

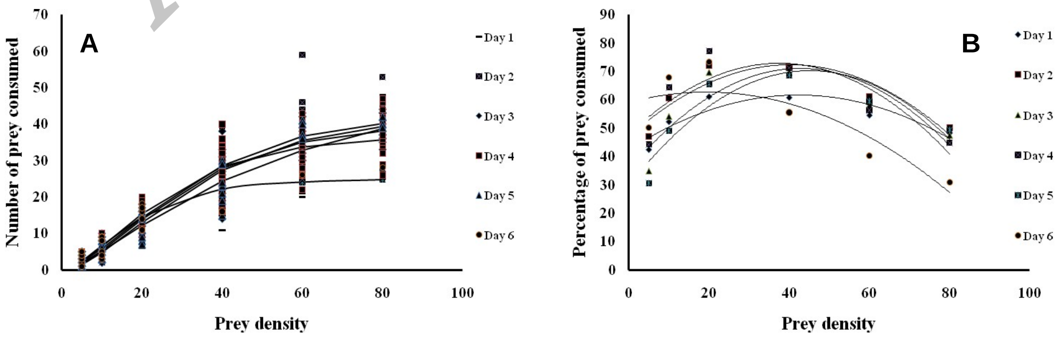

Fig. 1. Type III functional response (A) and percentage of predation (B) of the *Aphidoletes aphidimyza* larvae to the varying density of third instar nymphs of *Aphis craccivora* at different larval ages.

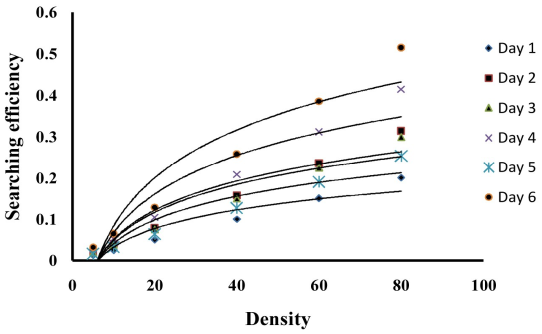

Fig. 2. Searching efficiency (*a'*) of *Aphidoletes aphidimyza* larval age to the varying density of third instar nymphs of *Aphis craccivora*.

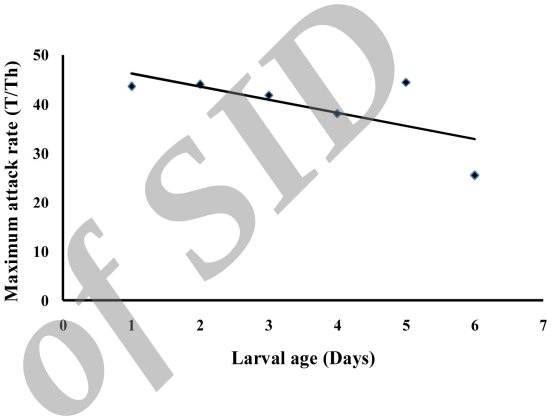

Fig. 3. Maximum attack rate of *Aphidoletes aphidimyza* larvae to the varying density of third instar nymphs of *Aphis craccivora* at different larval age.

Acknowledgments

We thank the authorities of the Faculty of Agricultural Sciences, University of Guilan, for their financial support and providing us with research facilities.

References

Ambrose, D. P., Claver, M. A. & Mariappan, P. (1996) Functional response of *Rhynocoris marginatus* Fabricius (Heteroptera: Reduvidae) to *Mylabris pustulata* (Coleoptera: Meloidae). *Fresenius Environmental Bulletin* 5, 85-89.

Asadi, R., Talebi, A. A., Khalghani, J., Fathipour, Y., Moharramipour, S. & Askari Siahooei, M. (2012) Age-specific functional response of *Psyllaephagus zdeneki* (Hymenoptera: Encyrtidae), parasitoid of *Euphyllura pakistanica* (Hemiptera: Psyllidae). *Journal of Crop Protection* 1, 1-15.

Asyakin, B. P. (1973) The use of aphidophagous gall-midge *Aphidoletes aphidimyza* Rondani (Dip.: Cecidomyiidae) in biological control of aphids in glasshouses. *Zapiski LSHI*, 212.

Atlihan, R. & Bora Kaydan, M. (2010) Functional response of the coccinellid predator, *Adalia fasciatopunctata revelierei* to walnut aphid (*Callaphis juglandis*). *Phytoparasitica* 38, 23-29.

Atlihan, R. & Chi, H. (2008) Temperature-dependent development and demography of *Scymnus subvillosus* (Coleoptera: Coccinellidae) reared on *Hyalopterus pruni* (Homoptera: Aphididae). *Journal of Economic Entomology* 101, 325-333.

Atlihan, R. & Güldal, H. (2009) Prey density-dependent feeding activity and life history of *Scymnus subvillosus*. *Phytoparasitica* 37, 35-41.

Badii, M. H., Hernández-Ortiz, E., Flores, A. & Landeros, J. N. (2004) Prey stage preference and functional response of *Euseius hibisci* to *Tetranychus urticae* (Acari: Phytoseiidae). *Experimental and Applied Acarology* 34, 263-273.

Bazzocchi, G. G. & Burgio, G. (2001) Functional response of *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) against *Aphis gossypii* Glover (Homoptera: Aphididae) at two constant temperatures. *Bolletino dell'Istituto di Entomologia "Guido Grandi" della Universita degli Studi di Bologna* 54, 13-21.

Casas, J. & McCauley, E. (2012) Daily foraging cycles create overlapping time-scales in functional responses. *Oikos* 121, 1966-1976.

Cave, R. D. & Gaylor, M. J. (1989) Functional response of *Telenomus reynoldsi* (Hym.: Scelionidae) at five constant temperatures and in an artificial plant arena. *Entomophaga* 34, 3-10.

Cédola, C. V., Sanchez, N. E. & Liliesthrom, G. G. (2001) Effect of tomato leaf hairiness on functional and numerical response of *Neoseiulus californicus* (Acari: Phytoseiidae). *Experimental and Applied Acarology* 25, 819-831.

Chen, K. R., Xu, Z. Y., Zhang, Z. Y., Fang, X. P. & Yan, L. Y. (1999) Biological characters and sequence analysis of coat protein gene of Chinese strains of peanut stripe virus (PStV). *Chinese Journal of Oil Crop Sciences* 21, 55-59.

Chen, W. L., Leopold, R. A. & Harris, M. O. (2006) Parasitism of the glassy-winged sharpshooter, *Homalodisca coagulata* (Homoptera: Cicadellidae): functional response and superparasitism by *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae). *Biological Control* 37, 119-129.

Chong, J. H. & Oetting, R. D. (2006a) Functional response and progeny production of the Madeira mealybug parasitoid, *Anagyrus* sp. nov. nr. *sinope*: the effect of host stage preference. *Biological Control* 41, 78-85.

Chong, J. H. & Oetting, R. D. (2006b) Host stage selection of the mealybug parasitoid *Anagyrus* sp. nov. nr. *sinope*. *Entomologia Experimentalis et Appllicata* 121, 39-50.

Coceano, P. G. & Peressini, S. (1989) Colonisation of maize by aphid vectors of barley yellow dwarf virus. *Annals of Applied Biology* 114, 443-447.

Cogni, R., Freitas, A. V. L. & Amaral Filho, B. F. (2002) Influence of prey size on predation success by *Zelus longipes* L. (Het.: Reduviidae). *Journal of Applied Entomology* 126, 74-78.

De Clercq, P., Mohaghegh, J. & Tirry, L. (2000) Effect of host plant on the functional response of the predator *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Biological Control* 18, 65-70.

De Jong, P. W. & van Alphen, J. J. M. (1989) Host size selection and sex allocation in *Leptomastix dactylopii*, a parasitoid of *Planococcus citri*. *Entomologia Experimentalis et Appllicata* 50, 161-169.

Ding-Xu, L., Juan, T. & Zuo-Rui, Sh. (2007) Functional response of the predator *Scolothrips takahashii* to hawthorn spider mite, *Tetranychus viennensis*: effect of age and temperature. *BioControl* 52, 41-61.

Dixon, A. F. G. & Agarwala, B. K. (2002) Triangular fecundity function and ageing in ladybird beetles. *Ecological Entomology* 27, 433-440.

El-Titi, A. (1973) Einflusse von Beutedichte und Morphologie der Wirtspflanze auf die Eiablage von *Aphidoletes aphidimyza* Rondani (Dip., Itonididae). *Zeitschrift für Angewandte Entomology* 72, 400-415.

Farhadi, R., Allahyari, H. & 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.

Fathipour, Y., Hosseini, A., Talebi, A. A. & Moharramipour, S. (2006) Functional response and mutual interference of *Diaeretiella rapae* (Hymenoptera: Aphidiidae) on *Brevicoryne brassicae* (Homoptera: Aphididae). *Entomologici Fennici* 17, 90-97.

Fernández-Arhex, V. & Corley, J. C. (2003) The functional response of parasitoids and its implications for biological control. *Biocontrol Science and Technology* 13, 403-413.

Garcia, J. F. & O'Neil, R. J. (2000) Effect of coleus size and variegation on attack rates, searching strategy, and selected life history characteristics of *Cryptolaemus montrouzieri* (Coleoptera: Coccinellidae). *Biological Control* 18, 225-234.

Godfray, H. C. J. (1994) *Parasitoids*: *behavioral and evolutionary ecology*. 473 pp. Princeton University Press.

González-Hernández, H., Pandey, R. R. & Johnson, M. W. (2005) Biological characteristics of adult *Anagyrus ananatis* Gahan (Hymenoptera: Encyrtidae), a parasitoid of *Dysmicoccus brevipes* (Cockerell) (Hemiptera: Pseudococcidae). *Biological Control* 35, 93-103.

Hassell, M. P. & Waage, J. K. (1984) Host-parasitoid population interactions. *Annual Review of Entomology* 29, 89-114.

Hassell, M. P., Lawton, J. H. & Beddington, J. R. (1977) Sigmoid functional response by invertebrate predators and parasitoids. *Journal of Animal Ecology* 46, 249-262.

Heidarian, M., Fathipour, Y. & Kamali, K. (2012) Functional response, switching, and prey-stage preference of *Scolothrips longicornis* (Thysanoptera: Thripidae) on *Schizotetranychus smirnovi* (Acari: Tetranychidae). *Journal Asia-Pacific Entomology* 15, 89-93.

Hodek, I. & Honek, A. (1996) *Ecology of Coccinellidae*. 464 pp. Dordrecht Boston London: Kluwer Academic.

Holling, C. S. (1966) Functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* 48, 1-87.

Joyce, A. L., Hoddle, M. S., Bellows, T. S. & González, D. (2001) Oviposition behavior of *Coccidoxenoides peregrinus*, a parasitoid of *Planococcus ficus*. *Entomologia Experimentalis et Applicata* 98, 49-57.

Juliano S. A. (1993) Nonlinear curve fitting: predation and functional response curves. pp. 159-182 in Scheiner, S. M. & Gurevitch, J. (Eds) *Design and analysis of ecological experiments*. 432 pp. Chapman and Hall, New York.

Kulp, D., Fortmann, M., Hommes, M. & Plate, H. P. (1989) Die räuberische Gallmücke *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) – Ein bedeutender Blattlausprädator – Nachschlagewerk zur Systematik, Verbreitung, Biologie, Zucht und Anwendung. *Mitteilungen aus der Biologischen Bundesanstalt für Land-und Forstwirtschaft Berlin-Dahlem* 250, 1-126.

Laing, J. E. & Osborn, J. A. L. (1974) The effect of prey density on functional and numerical response of three species of predatory mites. *Entomophaga* 19, 267-277.

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

Lester, P. J. & Harmsen, R. (2002) Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. *Journal of Applied Ecology* 39, 455-468.

Luck, R. F. (1985) Principles of arthropod predation. pp. 497-530 in Huffaker, C. B. & Rabb, R. L. (Eds) *Ecological entomology*. 756 pp. Wiley, New York.

Madadi, H., Enkegaard, A., Brodsgaard, H. F., Kharrazi-Pakdel, A., Mohaghegh, J. & Ashouri, A. (2007) Host plant effects on the functional response of *Neoseiulus cucumeris* to onion thrips larvae. *Journal of Applied Entomology* 131, 728-733.

Markkula, M., Hamalainen, M. & Forsberg, A. (1979) The aphid midge, *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) and its use in biological control of aphids. *Annales Entomologici Fennici* 45, 89-98.

Morse, J. G. (1981) Biological studies on *Aphidoletes aphidimyza* Rondani (Dip.: Cecidomyiidae) and its use in the biological control of the apple aphid *Aphis pomi* DeGeer (Hom.: Aphididae). Ph. D. Thesis. Michigan State University. E. Lansing, Michigan.

Morse, J. G. & Croft, B. A. (1987) Biological control of *Aphis pomi* (Hom.: Aphdidae) by *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae); a predator-prey model. *Entomophaga* 32, 339-356.

Parajulee, M. N., Shrestha, R. B., Leser, J. F., Wester, D. B. & Blanco C. A. (2006) Evaluation of the functional response of selected arthropod predators on bollworm eggs in the laboratory and effect of temperature on their predation efficiency. *Environmental Entomology* 35, 379-386.

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

Pettersson, J., Karunaratne, S., Ahmed, E. & Kumar, V. (1998) The cowpea aphid, *Aphis craccivora*, host plant odours and pheromones. *Entomologia Experimentalis et Applicata*, 88, 177-184.

Ponsonby, D. J. & Copland, M. J. W. (1998) Environmental influences on fecundity, egg viability and egg cannibalism in the scale insect predator, *Chilocorus nigritus*. *BioControl* 43, 39-52.

Priest, N. K., Mackowiak, B. & Promislow, D. E .L. (2002) The role of parental age effects on the evolution of aging. *Evolution* 56, 927-935.

Rabb, R. L. (1974) Naturally occurring biological control in the eastern United States, with particular reference to tobacco insects. pp. 294-309 in Huffaker, C. B. (Ed.) *Biological control*. 511 pp. Plenum Press, New York.

Rafiee Dastjerdi, H., Hejazi, M. J., Nouri Ganbalani, Gh. & Saber, M. (2009) Effects of some insecticides on functional response of ectoparasitoid, *Habrobracon hebertor* Say (Hym.: Braconidae). *Journal of Entomology* 6, 161-166.

Reis, P. R., Sousa, E. O., Teodoro, A. V. & Neto, M. P. (2003) Effect of prey densities on the functional and numerical response of two species of predaceous mites (Acari: Phytoseiidae). *Neotropical Entomology* 32, 461-467.

Reis, P. R., Teodor, A. V., Neto, M. P. & Silva, E. A. (2007) Life history of *Amblyseius herbicolus* (Acari: Phytoseiidae) on coffee plant. *Neotropical Entomology* 36, 282-287.

Rocha, L. da. & Redaelli, L. R. (2004) Functional response of *Cosmoclopius nigroannulatus* (Hem.: Reduviidae) to different densities of *Spartocera dentiventris* (Hem.: Coreidae) nymphs. *Brazilian Journal of Biology* 64, 309-316.

Rothstein, M. (1982) *Biochemical approaches to aging*. 314 pp. Academic Press, New York.

Ryoo, M. (1986) Studies on the basic component of the predation of *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Researches on Population Ecology* 28, 17-26.

Sabaghi, R., Sahragard, A. & Hosseini, R. (2011a) Functional and numerical response of *Scymnus syriacus* Marseul (Coleoptera: Coccinellidae) to the black bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae) under laboratory conditions. *Journal of Plant Protection Research* 51, 423-428.

Sabaghi, R., Sahragard, A. & Hosseini, R. (2011b) Area dependent searching efficiency of *Scymnus syriacus* (Col.: Coccinellidae) feeding on *Aphis craccivora* (Hem.: Aphididae). *Journal of Entomological Society of Iran* 31(1), 1-16.

Sabelis, M. W. (1992) Predatory arthropods. pp. 225-264 in Crawly, M. J. (Ed.) *Natural enemies*: *the population biology of predators*, *parasites, and diseases*. 576 pp. Blackwell Scientific Publications. Oxford London.

Sahragard, A. (1989) Biological studies on *Dicondylus indianus* Olmi (Hym.: Dryinidae) with particular reference to foraging behavior. Ph. D. Thesis. University of Wales, College of Cardiff, Wales, UK. 297 pp.

Sarmento, R. A., Pallini R., Venzon M., Fonseca de Souza, O. F., Molina-Rugama, A. J. & Lima de Oliveira, C. (2007) Functional response of the predator *Eriopis connexa* (Coleoptera: Coccinellidae) to different prey types. *Brazilian Archives of Biology and Technology* 50, 121-126.

SAS Institute (2001) *SAS/STAT user's guide*. SAS Institute Inc., Cary, NC Inc.

Seko, T. & Miura, K. (2008) Functional response of the lady beetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) on the aphid *Myzus persicae* Sulzer (Homoptera: Aphididae). *Applied Entomology and Zoology* 43, 341-345.

Shojaei, Sh., Safaralizadeh, M. H. & Shayesteh, N. (2006) Effect of temperature on the functional response of *Habrobracon hebetor* S. (Hymenoptera: Braconidae) to various densities of the host, *Plodia interpunctella* H. (Lepidoptera: Pyralidae). *Pakistan Entomologist* 28, 51-56.

Singh, S. R. & Jackai, L. E. N. (1985) Insect pests of cowpeas in Africa: their life cycle, economic importance, and potential for control. pp. 217-231 in Singh S. R. & Rachie, K. O. (Eds) *Cowpea research*, *production and utilization*. 488 pp. Wiley, Chichester.

Solomon, M. E. (1949) The natural control of animal populations. *Journal of Animal Ecology* 18, 1-35.

Srivastava, S. & Omkar (2004) Age-specific mating and reproductive senescence in the seven-spotted ladybird, *Coccinella septempunctata*. *The Journal of Applied Entomology* 128, 452-458.

Tahriri, S., Talebi, A. A., Fathipour, Y. & Zamani, A. A. (2007) Host stage preference, functional response and mutual interference of *Aphidius matricariae* (Hym.: Braconidae: Aphidiinae) on *Aphis fabae* (Hom.: Aphididae). *Journal of Entomological Science* 10, 323-331.

Taleb, M. A. & Sardar, M. A. (2007) Predation efficiency of insect predators in suppressing red mite, *Tetranychus bioculatus* attacking marigold. *Journal of Agriculture and Rural Development* 5, 98-104.

Timms, J. E., Oliver, T. H., Straw, N. A. & Leather, S. R. (2008) The effects of host plant on the coccinellid functional response: is the conifer specialist *Aphidecta obliterate* (L.) (Coleoptera: Coccinellidae) better adapted to spruce than the generalist *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae)? *Biological Control* 47, 273-281.

Trexler, J. C. & McCulloch, C. E., Travis, J. (1988) How can the functional response best be determined? *Oecology* 76, 206-214.

Trexler, J. C. & Travis, J. (1993) Nontraditional regression analysis. *Ecology* 74, 1629-1637.

Uygun, N. (1971) Der Einfluss der Nahrungsmenge auf Fruchtbarkeit und Lebensdauer von *Aphidoletes aphidimyza* Rond. (Diptera: Itonididae). *Zeitschrift für Angewandte Entomologie* 69, 234-258.

Varone, L., Bruzzone, O. & Logarzo, G. A. (2007) Egg limitation and the functional response of the parasitoid *Campoletis grioti* (Hym: Ichneumonidae). *Biocontrol Science and Technology* 17, 945-955.

Waage J. K. & Greathead D. J. (1988) Biological control: challenges and opportunities. *Philosophical Transactions of the Royal Society of London, Series B* 318, 111-128.

Warner, L. A. & Croft, B. A. (1982) Toxicities of azinphosmethyl and selected orchard pesticides to an aphid predator, *Aphidoletes aphidimyza*. *Journal of Economic Entomology* 75, 410-415.

Xiao, Y. & **Fadamiro, H. Y.** (2010) Functional responses and prey-stage preferences of three species of predacious mites (Acari: Phytoseiidae) on citrus red mite, *Panonychus citri* (Acari: Tetranychidae). *Biological Control* 53, 345-352.

Yaşar, B. & Özger, S. (2005a) Development, feeding and reproduction responses of *Adalia fasciatopunctata revelierei* (Mulsant) (Coleoptera: Coccinellidae) to *Hyalopterus pruni* (Geoffroy) (Homoptera: Aphididae). *Journal of Pest Science* 78, 199-203.

Yaşar, B. & Özger, S. (2005b) Functional response of *Oenopia conglobata* L. (Coleoptera: Coccinellidae) on *Hyalopterus pruni* Geoffroy (Homoptera: Aphididae) in three different size arenas. *Türkiye Entomoloji Derneği ve Dergisinin* 29, 91-99.

Zamani, A. A., Talebi, A. A., Fathipour, Y. & Baniameri, V. (2006) Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. *Journal of Pest Science* 79, 183-188.

Received: 21 September 2012
Accepted: 21 April 2013