

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

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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 $23 \pm 1^\circ\text{C}$, $70 \pm 5\%$ 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 صحرانگرد 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 قرار گرفت. آزمایش براساس واکنش تابعی وابسته به عمر نسبت به تراکم‌های مختلف (۵، ۱۰، ۲۰، ۴۰، ۶۰ و ۸۰) پوره‌های سن سوم *Aphis craccivora* (Koch) در شرایط $23 \pm 1^\circ\text{C}$ ، رطوبت نسبی $70 \pm 5\%$ و دوره‌ی نوری ۱۶:۸ 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 برآورد شده 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, $70 \pm 5\%$ 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, $70 \pm 5\%$ 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 ($15 \times 13 \times 3$ 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_a) 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):

$$N_a / N_0 = \exp (P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3) / [1 + \exp (P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)]$$

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:

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

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.,

Sarmiento *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).

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

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).

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*.

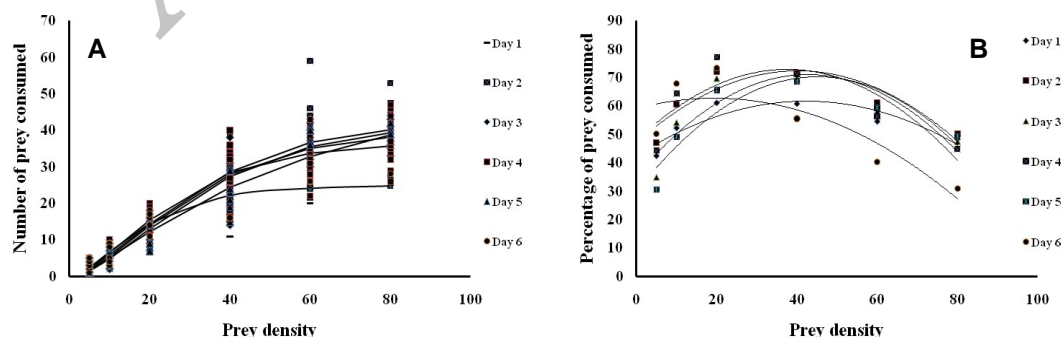


Fig. 1. Type III functional response (A) and percentage of predation (B) of the *Aphidoletes aphidimyza* larvae to the varying density of third instar nymphs of *Aphis craccivora* at different larval ages.

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

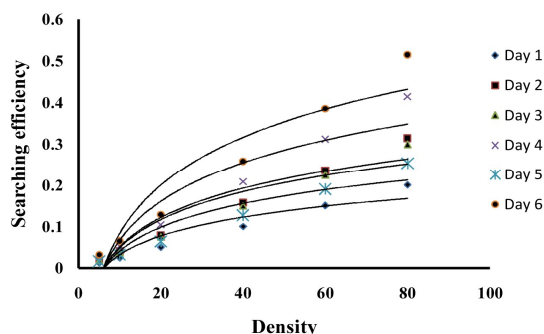
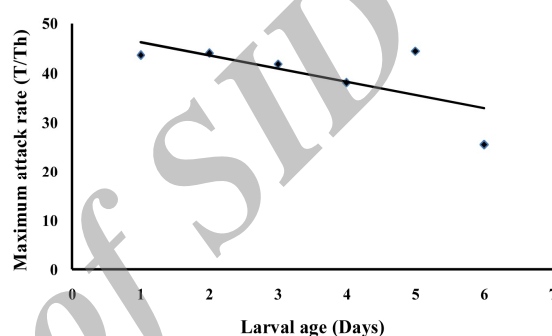


Fig. 3. Maximum attack rate of *Aphidoletes aphidimyza* larvae to the varying density of third instar nymphs of *Aphis craccivora* at different larval age.



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