JOURNAL OF ENTOMOLOGICAL SOCIETY OF IRAN
2017, 36(4): 239-248

Age-specific functional response of *Aphidius matricariae* and *Praon volucre* (Hym.: Braconidae) on *Aphis gossypii* (Hem.: Aphididae)

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Abstract

The cotton aphid, *Aphis gossypii* Glover is a major pest of greenhouse cucumber in the world. In this study, age specific functional response of *Aphidius matricariae* Haliday and *Praon volucre* (Haliday) were investigated on *A. gossypii* at 25±1°C, 60±5% RH and a photoperiod of 14 L: 10 D h. The results showed that the functional response of *A. matricariae* was type III during 1st, 2nd, 3rd, 4th and 5th days and type II in 6th day of adult parasitoid lifetime. The type of functional response of *P. volucre* was type II in whole parasitoid lifetime. The highest b value (0.02±0.003 h-1) and the lowest handling time (Th) (0.70±0.013 h) of *A. matricariae* were observed in the 1st day of parasitoid lifetime. The maximum attack rate (T/Th) of *A. matricariae* occurred in the first day of parasitoid lifetime (34.28 nymphs). The maximum searching efficiency of *P. volucre* was determined in the 2nd and 3rd days (0.03±0.003 and 0.03±0.005 h-1) and the minimum handling time was recorded in the 2nd day (0.97±0.140 h) of adult female life. The maximum parasitism rate was 24.74 nymphs in the two day old female, and then decreased in adult female age. The results suggest that *A. matricariae* and *P. volucre* are highly effective biological agents in suppressing *A. gosspii* population on cucumber in greenhouses.

Key words: Functional response, *Aphis gossypii*, parasitoid, cucumber

چکیده

واکنش تابعی وابسته به سن زنبورهای پارازیتویید *Aphidius matricariae* و *Praopn volucre* (Hym.: Braconidae) روی شته (Hem.: Aphididae) *Aphis gossypii*

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شته جالیز، *Aphis gossypii* Glover یکی از آفات مهم خیار گلخانه‌ای در جهان است. در این تحقیق واکنش تابعی وابسته به سن زنبورهای پارازیتویید *Aphidius matricariae* Haliday و *Praon volucre* (Haliday) روی شته *A. gossypii* در شرایط آزمایشگاهی ۱±۲۵ درجه سلسیوس، رطوبت نسبی ٪۵±۶۰ و دوره نوری ۱۴ ساعت روشنایی و ۱۰ ساعت تاریکی مورد بررسی قرار گرفت. نتایج نشان داد که واکنش تابعی زنبور *A. matricariae* در روزهای اول، دوم، سوم، چهارم و پنجم عمر زنبور پارازیتویید از نوع سوم و در روز ششم عمر از نوع دوم بود. واکنش تابعی زنبور پارازیتویید *P. volucre* در تمام عمر زنبور پارازیتویید از نوع دوم بود. بیشترین مقدار b (۰/۰۰۳±۰/۰۲ بر ساعت) و کمترین مقدار زمان دستیابی (Th) (۰/۰۱۳±۰/۷۰ ساعت) زنبور *A. matricariae* در روز اول عمر زنبور پارازیتویید بود. بیشترین مقدار حداکثر نرخ حمله زنبور پارازیتویید *A. matricariae* برابر ۳۴/۲۸ پوره و در روز اول عمر زنبور پارازیتویید مشاهده شد. بیشترین مقدار قدرت جستجوگری زنبور پارازیتویید *P. volucre* در روزهای دوم و سوم (۰/۰۰۳±۰/۰۳ و ۰/۰۰۵±۰/۰۳ بر ساعت، به ترتیب) عمر زنبورهای پارازیتویید ماده بدست آمد. کمترین زمان دستیابی زنبور پارازیتویید *P. volucre* برابر ۰/۱۴۰±۰/۹۷ ساعت و در روز دوم عمر زنبور پارازیتویید بود. همچنین بیشترین مقدار T/Th این زنبور پارازیتویید در روز دوم عمر و برابر ۲۴/۷۴ و در روز دوم عمر بدست آمد، سپس با افزایش عمر مقدار این پارامتر کاهش یافت. نتایج حاصل از این تحقیق نشان داد که دو گونه زنبور پارازیتویید *A. matricariae* و *P. volucre* می‌توانند به عنوان عوامل کنترل بیولوژیک مؤثر در کاهش جمعیت شته *A. gossypii* روی گیاه خیار در گلخانه‌ها در نظر گرفته شوند.

واژگان کلیدی: واکنش تابعی، *Aphis gosypii*، پارازیتویید، خیار

Introduction

The cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) has a worldwide distribution and is a major economically important pest of Cucurbitaceae, especially cucumber in greenhouses (Baniameri & Nasrollahi, 2003; van Emden & Harrington, 2007). This aphid causes direct damage by sucking the plant sap and indirectly damages its host through excreting honeydew and transmitting plant viruses (Blackman & Eastop, 2000). *Aphis gossypii* is a vector of 70 plant pathogenic

viruses such as the Cucumber Mosaic Virus (CMV) (Pinto *et al*., 2008). Chemical control of aphids in greenhouses are extremely difficult due to their high reproductive capability and resistance to insecticides (Gubran *et al*., 1993; Sadlo & Szpyrka, 2002; Bale *et al*., 2008; Perdikis et al., 2008).The cotton aphid has developed resistance to many commonly used insecticides (Gubran *et al*., 1993). Therefore, alternative techniques are necessary to effectively control of *A. gossypii* (Bale *et al*., 2008).

Biological control with the parasitoid wasps is one of the main control methods to manage the populations of *A. gossypii* in greenhouses (Hagvar & Hofsvang, 1991). All members of the subfamily Aphidiinae (Hymenoptera: Braconidae) are solitary endoparasitoids of aphids (Starý, 1970). They are among the most important natural enemies of aphids, which can effectively regulate the aphid populations and prevent serious outbreaks (Hagvar & Hofsvang, 1991). *Aphidius matricariae* Haliday and *Praon volucre* (Holiday) (Hymenoptera: Braconidae) are two effective parasitoid wasps of *A. gossypii* throughout the world (Stary *et al*., 2000; Zamani *et al*., 2006; Barahoei *et al*., 2014) That are commercially available against aphids in greenhouses (Hagvar & Hofsvang, 1991; Tazerouni *et al.*, 2016 a and b).

Response of individual parasitoid to increasing host density is one of the most important attributes that determines a parasitoid success in biological control programme. (Berryman, 1999; Timms *et al*., 2008). This behavioral feature referred to the functional response that defines the relationship between the number of preys or hosts attacked by a predator or parasitoid as a function of prey density (Solomon, 1949; Holling, 1959). Different abiotic and biotic factors such as temperature, prey or host species, natural enemy, physical conditions in the laboratory, host plant, age of pray or host, and age of parasitoid or predator influence the type and rate of functional response (Bellows, 1985; Fathipour *et al*., 2001; Mohaghegh *et al.*, 2001; Moezipour *et al*., 2008; Farhad *et al*., 2011; Asadi *et al*., 2012; Tazerouni *et al*., 2012; Nikbin *et al*., 2014; Pasandideh *et al*., 2015).

The scope of this research includes the effect of female parasitoid age on the type of functional response and efficiency and handling time of *A. matricariae* and *P. volucre* to various densities of *A. gossypii*.

Material and Methods

Insect cultures

Aphis gossypii was collected on cucumber in a greenhouse, located on the grounds of the College of Agriculture, Tarbiat Modares University, Tehran, Iran, in December 2012, and reared on potted young cucumber plants, Super Sultan variety.

The colony of *A. matricariae* was from mummies of *Myzus persicae* (Sulzer) collected from pepper and the colony of *P. volucre* was from mummies of *Acyrthosiphon pisum* (Harris) collected on *Vicia faba* L. (Leguminosae) in greenhouses of the Faculty of Agriculture, Tarbiat Modares University in Tehran, Iran, in spring 2013. The emerged adults of *A. matricariae* and *P. volucre* were reared on *A. gossypii* on potted cucumber plants, separately. The aphid and parasitoid colonies were reared at the temperature of 25±2°C, 60±5% RH and photoperiod of 14 L: 10 D h for several generations according to Kindlmann & Dixon (1989).

Experimental methods

The experimental arena consisted of a plastic container (15×13×5 cm) which covered with micromesh screen on the lid for ventilation. A detached cucumber leaf was placed into each container. The 3rd nymphal instars of A. *gossypii* (as preferred host stage for *A. matricariae* and *P. volucre*) (Tazerouni *et al*., 2016a) were randomly placed on the cucumber leaf inside the container at densities of 2, 4, 8, 16, 32 and 64 per container. A pair of male and female parasitoids (maximum 24 hours old) were placed into each container. Each host density was replicated 10 times. After 24 hours, the parasitoids (male and female) were removed and transferred into a new container containing another cucumber leaf that infested with aphids (at each host density separately). These experiments continued until 6th day of lifetime of *A. matricariae* and 4th day of lifetime of *P. volucre*. The exposed aphids (at each density and at each day separately) remained under experimental conditions (25±1°C, 60±5% RH and a photoperiod of 14 L: 10 D h) until formation of aphid mummies. Then the mummified aphids were counted at each density per day, separately. The data of the last day of lifetimes of two parasitoids was notc counted to avoid unwanted abnormal output due to the death of most female parasitoid individuals. Honey-water solution (20%) was provided for adult parasitoids.

Statistical analysis

The data of functional responses were analyzed in two separate steps. In the first step, the type of functional response was determined by logistic regression analysis of the proportion of parasitized host (N_a) in relation to initial host density (N_0). The data were fitted by a logistic regression model which describes the relationship between N_a / N_0 and N_0 (Juliano, 2001):

$$\frac{N_a}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^{\,2} + P_3 N_0^{\,3})}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^{\,2} + P_3 N_0^{\,3})}$$

Where N_a is the number of parasitized hosts, N_0 is the initial host density and P_0, P_1, P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively (Juliano, 2001). These parameters were estimated using the method of maximum likelihood.

Significant negative or positive linear coefficients (P_1) indicate type II or III functional responses, respectively. A negative linear parameter (P_1) indicates that the proportion of parasitized host declines monotonically with the initial number of host available, thus functional response is type II. If $P_1 > 0$, the proportion of parasitized host is positively density-dependent, thus describing a type III functional response (Juliano, 2001; De Clercq *et al*. 2000).

After determining the type of functional response, handling time (T_h) and searching efficiency (a) were estimated by random parasitoid model as follows (Royama, 1971; Rogers 1972; Hassell *et al*., 1977; Juliano 2001):

$$N_a = N_t \left[1 - \exp\left\{ - \frac{aTP_t}{1 + a T_h N_t} \right\} \right]$$

Where N_a is the number of parasitized hosts, N_t is the number of host available, T is the total time of the experiment, a is the searching efficiency, P_t is the number of parasitoid and T_h is the handling time. For type III functional response, the searching efficiency (a) is set as a function of host density. This parameter is calculated using the following equation:

$$a = \frac{d + b N_0}{1 + c N_0} \qquad \text{(Full model)}$$

$a = d + bN_0$ if c=0 (Reduced model 1)

$a = bN_0$ if c=0, d=0 (Reduced model 2)

The parameters b, c and d are constants. The simple model of $a = bN_0$ is used for estimating the searching efficiency because the parameters c and d are not significantly different from zero.

The SAS software was used for statistical analyses (SAS Institute, 2003). Statistical comparisons in different days of parasitoid age were made possible using SPSS 18.1 software with Tukey tests ($P < 0.05$) (SPSS, 2009). Three-dimensional contour plot was drawn using the MATLAB software (MATLAB, 2009) to show three variables (parasitoid age, host density and percentage of parasitism) at a time.

Results

Results of logistic regression to distinguish between type II and III functional responses are shown in Table 1 and 2. The functional response of *A. matricariae* was type III during 1st, 2nd, 3rd, 4th and 5th days of parasitoid lifetime because the value of linear coefficient ($P_1 > 0$) was positive (Table 1) that suggests that the proportion of parasitized hosts, at lower host densities, increases as the host density increases (Figure 1 and 2). The functional response of *A. matricariae* in the 6th day of parasitoid lifetime was type II. According to significant negative linear coefficients ($P_1 < 0$) of the logistic regression model (Table 1), proportion of parasitized hosts declined with increasing host density (Figure 1 and 2). The slope of regression line in the 6th day of parasitoid lifetime shows low parasitism rate for *A. matricariae* (Figure 1). Figure 2 shows the effect of host density and parasitoid lifetime on the percentage of parasitism rate of *A. gossypii* by *A. matricariae* in three-dimensional contour plot. The highest percentage of parasitism of third instar nymphs of *A. gossypii* by *A. matricariae* occurred in the first day of parasitoid lifetime and at host densities of 8 and 16.

Data fitted to the logistic regression revealed significant negative linear coefficient ($P_1 < 0$) for hosts parasitized by *P. volucre*, which indicated a type II functional response through parasitoid lifetime (Table 2). Type of functional response was not affected by female ages of *P. volucre*. This means that proportion of parasitized host decreased with increasing host density (Figure 3 and 4). The maximum percentage of parasitism of 3rd nymphs of *A. gossypii* by *P. volucre* was observed in the 2nd and 3rd days of parasitoid lifetime at low host densities (densities of 2 and 4 nymphs of aphid) (Figure 4).

Results of nonlinear least square regression in type III functional response indicated that the parameters c and

d were not significantly different from zero , therefore, we used the simple model $a= bN_0$ to estimate searching efficiency at each density. The highest *b* value (0.02±0.003 h^{-1}) and the lowest handling time (T_h) (0.70±0.013 h) were observed in the 1st day of parasitoid lifetime (Table 3). The *b* value for parasitized hosts declined with the age of parasitoid. The maximum attack rate (T/T_h) of *A. matricariae* was highest at the first day (34.28 nymphs) and was minimum at the 6th day of parasitoid lifetime (4.89 nymphs) (Table 3).

The estimated values of searching efficiency (a), handling time (T_h), maximum attack rate (T/T_h) and efficiency (a/T_h) in *P. volucre* are shown in Table 4. The highest searching efficiency (a) was recorded on the 2nd and 3rd days (0.03±0.003 and 0.03±0.005 h^{-1}, respectively) of parasitoid life. The minimum handling time (T_h) was 0.97±0.140 h on the 2nd day of adult female life. The maximum parasitism rate (T/T_h) was 24.74 nymphs on the 2nd day old female, then it decreased by adult female age. The highest and lowest efficiency (a/T_h) of *P. volucre* on the 3rd nymphal instar of *A. gossypii* was in the 2nd (0.031) and 4th (0.004) days old female parasitoid, respectively (Table 4).

Table 1. Results of logistic regression analysis of the proportion of *Aphis gossypii* third nymphs parasitized by *Aphidius matricariae* adults as a function of initial host density at different ages of life

Female parasitoid age (Days)		Parameter			
		P_0	P_1	P_2	P_3
1		0.92±0.235	0.07±0.006	-0.003±0.001	$3\times10^{-5}\pm1\times10^{-5}$
	χ^2	4.52	1.06	1.69	1.39
	P	0.034	0.302	0.194	0.238
2		0.20±0.038	0.05±0.006	$-0.002\pm2\times10^{-4}$	$1\times10^{-5}\pm2\times10^{-6}$
	χ^2	0.28	0.75	0.62	0.30
	P	0.594	0.387	0.430	0.585
3		0.008±0.003	0.02±0.006	$-5\times10^{-4}\pm2\times10^{-4}$	$5\times10^{-6}\pm2\times10^{-6}$
	χ^2	0.01	0.13	0.05	0.01
	P	0.983	0.720	0.815	0.998
4		-0.54±0.038	0.05±0.006	$-0.001\pm2\times10^{-4}$	$6\times10^{-6}\pm2\times10^{-6}$
	χ^2	2.02	0.75	0.35	0.09
	P	0.155	0.388	0.556	0.766
5		-1.16±0.45	0.03±0.007	$-9\times10^{-4}\pm2\times10^{-4}$	$6\times10^{-6}\pm3\times10^{-6}$
	χ^2	6.64	0.16	0.14	0.07
	P	0.010	0.690	0.710	0.788
6		-1.11±0.071	-0.01±0.001	$0.004\pm4\times10^{-4}$	$-4\times10^{-5}\pm5\times10^{-6}$
	χ^2	2.44	1.18	0.89	0.88
	P	0.118	0.278	0.346	0.348

Table 2. Results of logistic regression analysis of the proportion of *Aphis gossypii* third nymphs parasitized by *Praon volucre* adults as a function of initial host density at different ages of life

Female parasitoid age (Days)		Parameter			
		P_0	P_1	P_2	P_3
1		-0.85±0.418	-0.03±0.006	$0.001\pm2\times10^{-4}$	$-1\times10^{-5}\pm2\times10^{-6}$
	χ^2	4.12	0.29	0.24	0.31
	P	0.042	0.592	0.623	0.576
2		0.04±0.003	-0.06±0.005	$0.001\pm2\times10^{-4}$	$-1\times10^{-5}\pm2\times10^{-6}$
	χ^2	0.01	1.11	0.36	0.25
	P	0.916	0.291	0.550	0.618
3		-0.41±0.039	-0.03±0.006	$5\times10^{-4}\pm2\times10^{-5}$	$-5\times10^{-6}\pm1\times10^{-6}$
	χ^2	1.14	0.27	0.05	0.06
	P	0.285	0.600	0.817	0.806
4		-1.55±0.493	$-0.007\pm7\times10^{-4}$	$4\times10^{-4}\pm3\times10^{-5}$	$-7\times10^{-6}\pm3\times10^{-6}$
	χ^2	9.86	0.01	0.02	0.06
	P	0.002	0.922	0.891	0.800

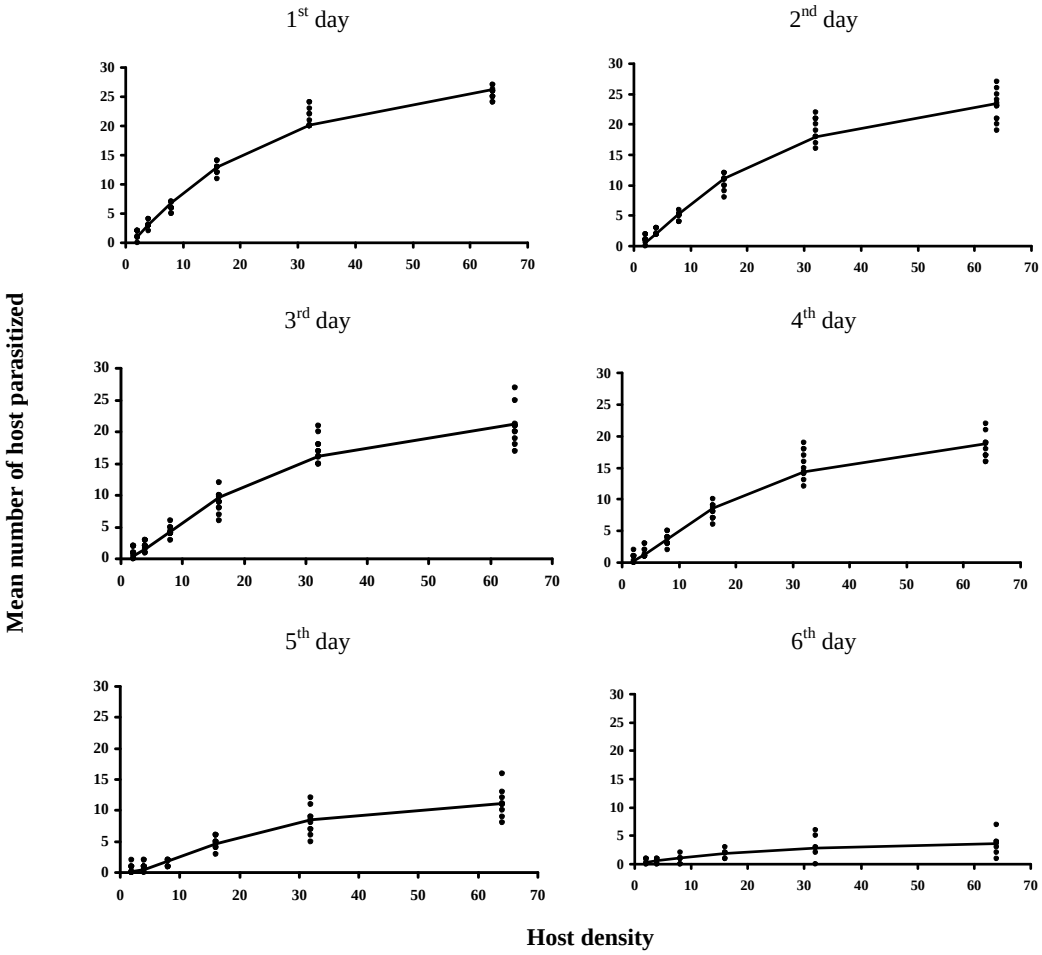

Fig. 1. Age specific functional response of *Aphidius matricariae* on different densities of third instar nymphs of *Aphis gossypii* on cucumber (Super Sultan variety)

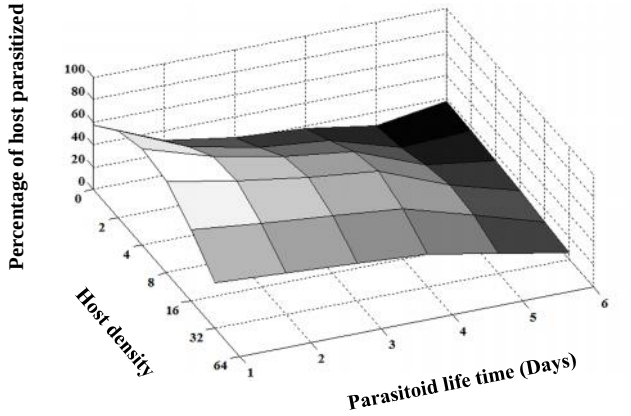

Fig. 2. Three-dimensional contour plot showing the effect of parasitoid life time and host density on the percentage of parasitism by *Aphidius matricariae*.

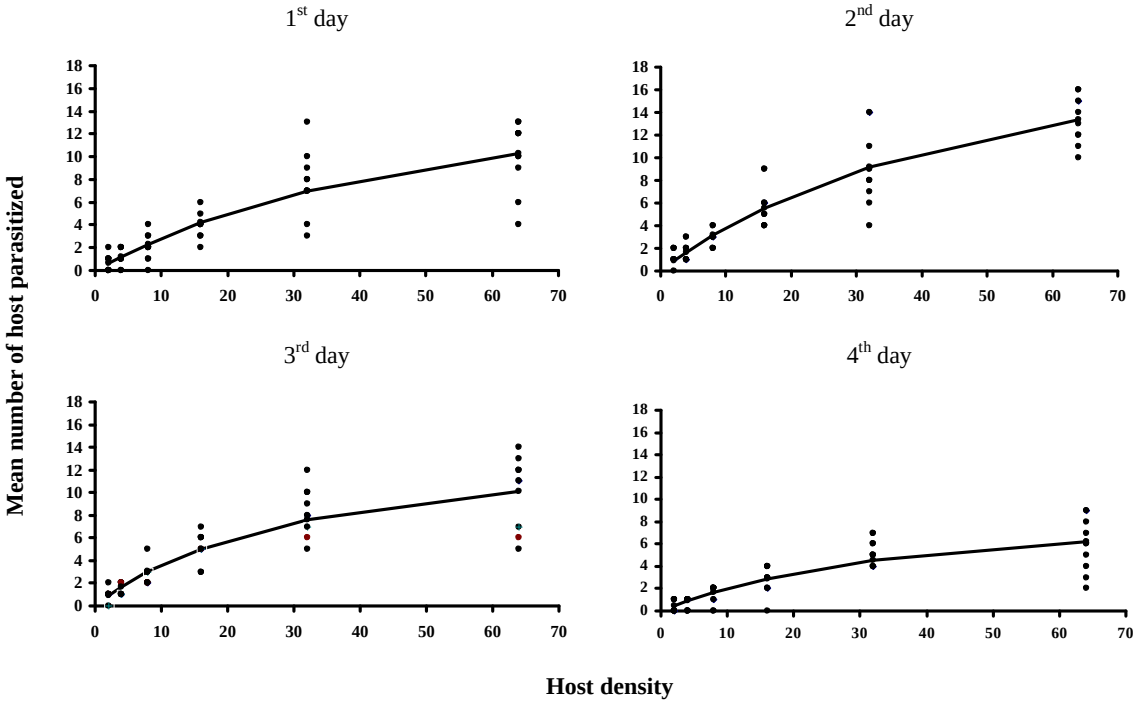

Fig. 3. Age specific functional response of *Praon volucre* on different densities of third instar nymphs of *Aphis gossypii* on cucumber (Super Sultan variety).

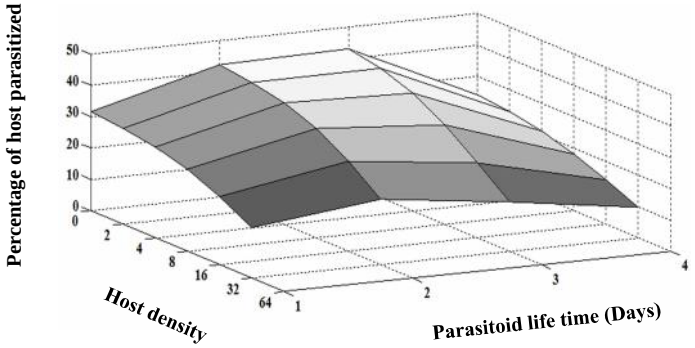

Fig. 4. Three-dimensional contour plot showing the effect of parasitoid life time and host density on the percentage of parasitism by *Praon volucre*.

Table 3. Estimates (±SE) parameters (including searching efficiency (a), handling time (T_h), maximum attack rate (T/T_h) and a/T_h values) by Rogers type II or III equations, indicating the functional response of *Aphidius matricariae* females of different ages on third nymph instars of *Aphis gossypii* on cucumber (Super Sultan variety)

Female parasitoid age (Days)	Parameter				
	a (h^{-1})	b ($a= bN_0$)	T_h (h)	T/T_h	a/T_h
1	0.04-1.28	0.02±0.003	0. 70±0.013	34.28	0.057-1.828
2	0.016-0.512	0.008±0.001	0.79±0.022	30.38	0.020-0.648
3	0.01-0.32	$0.005±8\times10^{-4}$	0.88±0.031	27.27	0.011-0.364
4	0.008-0.256	$0.004±6\times10^{-4}$	1.02±0.035	23.53	0.008-0.251
5	0.004-0.128	$0.002±3\times10^{-4}$	1.81±0.101	21.82	0.002-0.071
6	0.008±0.002	-	4.50±1.529	4.89	0.002

a ($a =bN_0$) is the searching efficiency in functional response type III. This parameter in functional response type III is different at each density.

Table 4. Estimates (±SE) parameters (including searching efficiency (a), handling time (T_h), maximum attack rate (T/T_h) and a/T_h values) by Rogers type II equations, indicating the functional response of *Praon volucre* females of different ages on third nymph instars of *Aphis gossypii* on cucumber (Super Sultan variety).

Female parasitoid age (Days)	Parameter			
	a (h^{-1})	T_h (h)	T/T_h	a/T_h
1	0.02±0.003	1.20±0.248	20	0.017
2	0.03±0.003	0.97±0.140	24.74	0.031
3	0.03±0.005	1.59±0.194	15.09	0.019
4	0.01±0.002	2.38±0.419	10.08	0.004

Discussion

According to the both parasitoid wasps (*A. matricariae* and *P. volucre*) can be effectively used in the biological control of *A. gossypii* on cucumber (Super Sultan variety). *A. matricariae* and *P. volucre* caused a high mortality on the host by parasitizing 34.28 and 24.74 host nymphs, respectively, during 24 h. The functional response of *A. matricariae* and *P. volucre* on different aphid species are reported in previous studies in foraging period of 24 h (Talebi *et al*., 2006; Zamani *et al*., 2006; Tahriri *et al*., 2007; Farhad *et al*., 2011), but the age specific functional response has received little attention (Pasandideh *et al*., 2015; Tazerouni *et al*., 2016 b).

The type of functional response of *A. matricariae* varied between type II and III in different ages of parasitoid lifetime, but in *P. volucre* was not affected by female ages and was type II in whole parasitoid lifetime. A type II functional response leads to inverse density-dependent predation or parasitism. In turn, the type III functional response leads to direct density dependence as predation or parasitism rate increases at low host densities, and then decreases at higher host densities with an s-shape response curve that potentially regulates the host population (Berryman, 1999; Bernstein, 2000). Both type II (Zamani *et al*., 2006; Farhad *et al*., 2011; Tazerouni *et al*., 2012; Pasandideh *et al*., 2015; Tazerouni *et al*., 2016 b) and type III of functional responses had been mentioned for parasitoid wasp species of Aphidiinae (van Steenis & El-Khawass 1995; Rakhshani *et al*., 2004; Tazerouni *et al*., 2016 b), although type II of functional response is more frequent in parasitoids (Fernández-arhex & Corley, 2003).

The maximum efficiency of both parasitoids based on the searching efficiency and handling time was obtained from 1st to 3rd days of female parasitoid age. Lower handling time and higher searching efficiency of parasitoid wasps, at younger ages of parasitoids, were observed in previous studies (Bellows, 1985; Asadi *et al*., 2012; Nikbin *et al*., 2014; Pasandideh *et al*., 2015; Tazerouni *et al*., 2016 b). In this study, handling times for *A. matricariae* and *P. volucre* were 0.70 and 1.20 h, respectively in the first day of parasitoid lifetime. The handling time value for *A. matricariae* was lower comparing to the findings by Zamani *et al*. (2006) for *A. colemani* and *A. matricariae* (1.03 and 1.01 h on *A. gossypii*, respectively) and Tahriri *et al*. (2007) for *A. matricariae* (3.439 h on *Aphis fabae* (Scopoli)). The handling time value for *P. volucre* was higher in comparison with the aphid hosts such as *Sitobion avenae* (F.) (1.02 h) (Farhad *et al*., 2011), *Acyrthosiphon pisum* (Harris) (0.51 h) (Pasandideh *et al*., 2015) and *M. persicae* (0.51 h) (Tazerouni *et al*., 2016 b). The differences among results of this study with other researches indicate that existing variation within host species, host plants and experimental conditions affect the efficiency of these two parasitoid species. .

We can conclude that *A. matricariae* and *P. volucre* are efficient biological control agents against *A. gossypii* on cucumber (Super Sultan variety) in greenhouses, although additional studies on demographic parameters and other foraging behavior of these parasitoids are required.

Acknowledgments

We would like to thank the Department of Entomology, Tarbiat Modares University, for providing financial support for this research and to thank the two anonymous reviewers for their valuable comments and suggestions on the manuscript.

References

Asadi, R., Talebi, A. A., Khalaghani, 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), 1-15.

Bale, J. S., van Lenteren, J. C. & Bigler, S. (2008) Biological control and sustainable food production. *Philosophical Transactions of the Royal Society B-Biological Science* 363, 761-776.

Baniameri, V. & Nasrollahi, A. A. (2003) Status of IPM Program in Greenhouse Vegetables in Iran. *IOBC/WPRS Bulletin*, Additional Abstracts/Papers 26, 1–3.

Barahoei, H., Rakhshani., E, Nader, E., Stary, P., Kavallieratos, N. G., Tomanović, Z. & Mehrparvar, M. (2014) Checklist of Aphidiinae parasitoids (Hymenoptera: Braconidae) and their host aphid associations in Iran. *Journal of Crop Protection* 3 (2), 199-232.

Bellows, T. S. (1985) Effect of host and parasitoid age on search behaviour and oviposition rates in *Lariopahagus distinguendus* Forster (Hymenoptera: Peteromalidae). *Researches on Population Ecology* 27, 65-76.

Bernstein, C. (2000) Host-parasitoid models. pp. 41-57 in Hochberg, M. & Ives, A. (Eds.) *The story of successful failure, in Population Biology of Host/Parasitoid Interactions*, Princeton University Press, Princeton, NJ.

Berryman, A. A. (1999) The Theoretical Foundations of Biological Control. pp. 3-21 in Hawkins, B. A. & Cornell, H. V. (Eds.) *Theoretical Approaches to Biological Control*, Cambridge University Press.

Blackman, R. L. & Eastop, V. P. (2000) *Aphids on the world crop pests*. 475 pp. John Wiley and Sons, London.

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

Farhad, A., Talebi, A. A. & Fathipour, Y. (2011) Foraging behavior of *praon volucre* (Hymenoptera: Blaconidae) a parasitoid of *sitibion avanae* (Hemiptera: Aphididae) on wheat. *Psyche*, 1-7.

Fathipour, Y., Kamali, K., Khalaghani, J. & Abdollahi, G. (2001) Functional response of *Trissolcus grandis* (Hymenoptera: Scelionidae) to different egg densities of *Eurygaster integriceps* (Heteroptera: Scutelleridae) and effects of wheat genotypes on it. *Journal of Applied Entomology and Phytopathology* 68, 123-136.

Fernández-arhex, V. & Corley, J. C. (2003) The Functional Response of Parasitoids and its Implications for Biological Control. *Biocontrol Science and Technology* 13 (4), 403-413.

Gubran, E. M. E., Delorme, R., Auge, D. & Moreau, J. E. (1993) Pyrethroids and organochlorines resistance in cotton aphid *Aphis gossypii* (Glov.) (Homoptera, Aphididae) in the Sudan Gezira. *International Journal of Pest Management* 39, 197-200.

Hagvar, E. B., & Hofsvang, T. (1991) Aphid parasitoids (Hymenoptera: Aphidiidae): biology, host selection, and use in biological control. *Biocontrol News and Information* 12, 13–41.

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.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91, 385-398.

Juliano, S. A. (2001) Nonlinear curve-fitting: predation and functional response curves. pp. 178–196 in Scheiner, S. M. & Gurevitch, J. (Eds) *Design and Analysis of Ecological Experiments*, 2nd ed. Oxford University Press, New York.

Kindlmann, P. & Dixon, A. F. G. (1989) Development constraints in the evolution of reproductive strategies: telescoping of generations in parthenogenetic aphids. *Functional Ecology* 3, 531-537.

MATLAB. (2009) MATLAB: the language of technical computing, version 7.8. The MathWorks Incorporation, MI.

Moezipour, M., Kafil, M. & Allahyari, H. (2008) Functional response of *Trichogramma brassicae* at different temperatures and relative humidities. *Bulletin of Insectology* 62(2), 245-250.

Mohaghegh, J., DeClercq, P. & Tirry, L. (2001) Functional response of the predators *Podisus maculiventris* (Say) and *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) to the beet Armyworms, *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae): effect of temperature. *Journal of Applied Entomology* 125, 131- 134.

Nikbin, R., Sahragard, A. & Hosseini, M. (2014) Age-specific functional response of *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) parasitizing different egg densities of *Ephestia kuehniella* (Lepidoptera: Pyralidae). *Journal of Agricultural Science and Technology* 16, 1205-1216.

Pasandideh, A., Talebi, A. A., Hajiqanbar, H. & Tazerouni, Z. (2015) Host stage preference and age-specific functional response of *Praon volucre* (Hymenoptera: Braconidae, Aphidiinae) a parasitoid of *Acyrthosiphon pisum* (Hemiptera: Aphididae). *Journal of Crop Protection* 4 (4), 563-575.

Perdikis, D., Kapaxidi, E. & Papadoulis, G. (2008) Biological control of insect and mite pests in greenhouse solanaceous crops. *The European Journal of Plant Science and Biotechnology* 2 (1), 125-144.

Pinto, Z. V., Rezende, J. A. M., Yuki, V. A. & Piedade, S. M. S. (2008) Ability of *Aphis gossypii* and *Myzus persicae* to transmit cucumber mosaic virus in single and mixed infection with two Potyviruses to zucchini squash. *Summa Phytopathologica* 34 (2), 183-185.

Rakhshani, E., Talebi, A. A., Kavallieratos, N. & Fathipour, Y. (2004) Host stage preference, juvenile mortality and functional response of *Trioxys pallidus* (Hymenoptera: Aphidiinae). *Biologia* 59, 197–203.

Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology* 41, 369-383.

Royama, T. (1971) A comparative study of models for predation and parasitism. *Researches on Population Ecology, Supplement* 1, 1-91.

Sadlo, S. & Szpyrka, E. (2002) Pesticide residues in greenhouse vegtebles of south-eastern Poland in 1999-2001. *Journal of Plant Protection Research* 42, 181-188.

SAS Institute (2003) GLM: A Guide to Statistical and Data Analysis, version 9.1. SAS Institute, Cary, NC.

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

SPSS (2009) SPSS base18.0 users guide. SPSS, Chicago, IL.

Starý, P. (1970) *Biology of aphid parasites (Hymenoptera: Aphidiidae) with respect to integrated control*. 643 pp. Series entomologica. Publishers, The Hague.

Stary, P., Remaudière, G., González, D. & Shahrokhi, S. (2000) A review and host associations of aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) of Iran. *Parasitica* 56, 15-41.

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). *Entomological Science* 10, 323-331.

Talebi, A. A., Zamani, A. A., Fathipour, Y., Baniameri, V., Kheradmand, K. & Haghani, M. (2006) Host stage preference by *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae) as parasitoids of *Aphis gossypii* (Hemiptera: Aphididae) on greenhouse cucumber. Integrated Control in Protected Crops, Mediterranean Climate. *IOBC/Wprs Bulletin* 29, 173–177.

Tazerouni Z, Talebi A. A. & Rakhshani, E. (2012) Temperature-dependent functional response of *Diaeretiella rapae* (Hymenoptera: Braconidae), a parasitoid of *Diuraphis noxia* (Hemiptera: Aphididae). *Journal of the Entomological Research Society* 14(1), 31-40.

Tazerouni Z., Talebi A. A., Fathipour Y. & Soufbaf, M. (2016 a) Interference competition between *Aphidius matricariae* and Praon volucre (Hymenoptera: Braconidae) attacking two common aphid species. *Biocontrol Science and Technology* 26 (11), 1552-1564.

Tazerouni, Z., Talebi, A. A., Fathipour, Y. & Soufbaf, M. (2016 b) Age-specific functional response of *Aphidius matricariae* and *Praon volucre* (Hymenoptera: Braconidae) on *Myzus persicae* (Hemiptera: Aphididae). *Neotropical Entomology*, 642-651.

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.

van Emden, H. F. & Harrington, R. (Eds.). (2007). *Aphids as crop pests*. CABI, Wallingford, United Kingdom.

van Steenis, M. J. & EL-Khawass K. A. M. H. (1995) Behaviour of *Aphidius colemani* searching for *Aphis gossypii*: functional response and reaction to previously searched aphid colonies. *Biocontrol Science and Technology* 5, 339-347.

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: 6 November 2016
Accepted: 23 January 2017