

Age-specific Functional Response of *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) Parasitizing Different Egg Densities of *Ephestia kuehniella* (Lepidoptera: Pyralidae)

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ABSTRACT

The parasitoid *Trichogramma brassicae* Bezenko is used for inundative releases in biological control programs against lepidopteran pests in agro-ecosystems. Age-specific functional responses of *T. brassicae* to different egg densities (5, 10, 20, 30, 40, 60, and 80) of sterilized eggs of *Ephestia kuehniella* at $23\pm 1^{\circ}\text{C}$, $60\pm 5\%$ RH, and 16:8 h (L:D photoperiod) were studied. *E. kuehniella* densities were separately presented to a single mated female of *T. brassicae* (1-day-old). The egg densities were replaced every day until the parasitoid died and each density was replicated 20 times. A type III functional response was obtained for the one-day-old females and a type II for two- to nine-day-old ones. Results show that parasitoid age influences searching efficiency and handling time. Searching efficiency (a') varied as adult parasitoids aged. In contrast, handling time increased with age. The lowest and highest values were obtained in days 1 and 9 of the parasitoid's life, respectively. The maximum rate of parasitism (T/T_h) decreased significantly with an increase in parasitoid age. It was concluded that *T. brassicae* females were most efficient at early ages of their life and might be capable of efficiently suppressing lepidopteran pest populations.

Keywords: Age-specific parasitism, Biological control, Host density, Parasitoid, Search rate.

INTRODUCTION

In recent years, as the negative side effects of insecticides have increased, usage of natural enemies appears to be very helpful in biological control programs (Atlihan and BoraKaydan, 2010). One of the tactics that has proved to be suitable in biological control programs, particularly for lepidopteran pests, is the release of egg parasitoids (Parra and Zucchi, 2004). Among these parasitoids, wasps of the genus *Trichogramma* (Hymenoptera: Trichogrammatidae) have shown promising results (Bueno *et al.*, 2009). *Trichogramma* spp. have additional advantages, such as easy rearing on alternative hosts, which

allow them to be used in inundative releases for the control of key pests of several crops (Parra and Zucchi, 2004). Their inundative releases are being used in biological control of agricultural pests in cotton, maize, sugarcane, vegetables, and fruits in more than 30 countries worldwide (Li, 1994; Smith, 1996). *Trichogramma* species present some advantages that make them well-suited for use in inundative releases against some key pests occurring in Iran, such as the rice stem borer, *Chilo suppressalis* (Walker), the European corn stem borer, *Ostrinia nubilalis* (Hübner), and the carob moth, *Ectomyelois ceratoniae* (Zeller) in Iran (Ebrahimi *et al.*, 1998). *T. brassicae* Bezenko (Hymenoptera: Trichogrammatidae) is the

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most widespread species in Iran (Azema and Mirabzadeh, 2005).

Before using a parasitoid in a biological control program, it is necessary to have information on its efficiency (Jervis and Kidd, 1996). An important aspect to assess the efficiency of a natural enemy is its attack rate and searching behavior when exposed to a broad range of host densities, i.e. its functional response (Berryman, 1999; Badii *et al.*, 2004; Fathipour *et al.*, 2006; Timms *et al.*, 2008) which relates to the impact of insect parasitoids and predators on varying density of host or prey (Solomon, 1949; Holling, 1959). The functional response is an important key to understanding how parasitoids or predators influence the population dynamics of their hosts or prey and how they affect the structure of the communities in which they live (Jervis and Kidd, 1996; Wajnberg *et al.*, 2008). Functional response studies also provide information on host-finding abilities of candidate natural enemies (Munyaneza and Obrycki, 1997). A functional response is characterized by two parameters: the handling time (T_h), the time taken for a parasitoid to encounter and parasitize a single host; and the attack rate or searching efficiency (a'), the rate at which functional response increases with host density (Hassell, 1978). Holling (1959, 1966) considered three types of functional responses: type I, a linear rise to a plateau; type II, a curvilinear rise to a plateau; and type III, a sigmoid curve rising to a plateau determined by handling time or satiation (Berryman, 1999; Hassell, 2000). The type and rate of a functional response are affected by different abiotic and biotic factors such as the temperature, the prey or host species, the natural enemy, the physical conditions in the laboratory, the host plant and the age of the parasitoid (Coll and Ridgway, 1995; Messina and Hanks, 1998; Mohaghegh *et al.*, 2001; Fathipour *et al.*, 2001; Allahyari *et al.*, 2004; Kalyebi *et al.*, 2005; Reay-Jones *et al.*, 2006; Moezipour *et al.*, 2008; Asadi *et al.*, 2012).

Type I (Mills and Lacan, 2004) and II functional responses (Smith, 1996) and even type III have also been shown for *Trichogramma* wasps (Wang and Ferro, 1998). Moezipour *et al.* (2008) reported different types of functional responses for *T. brassicae* at different temperatures and relative humidities. A type II functional response for both *Wollbachi*-infected and un-infected strains of *T. brassicae* have also been observed (Farrokhi *et al.*, 2010). Arbab Tafti *et al.* (2004) found a type III functional response for *T. brassicae* against *Sitotroga cerealella* Olivier. A type III response was also demonstrated by Farazmand and Iranipour (2006) on *Ephestia kuehniella* Zell. and *Plodia interpunctella* Hub. Furthermore, in the study reported by Reay-Jones *et al.* (2006), *T. chilonis* displayed functional responses of types III and II to different densities of *Galleria mellonella* L. and *Chilo sacchariphagus* Bojer., respectively.

This is the first study intended to evaluate how age influences the efficiency of female *T. brassicae*, its type of functional, its lifetime searching efficiency, and handling times.

MATERIALS AND METHODS

Parasitoid and Host Rearing

Eggs of *S. cerealella* parasitized by *T. brassicae* were obtained from Biological Control Research Department (BCRD) of the Iranian Research Institute of Plant Protection (IRIPP). After the adults had emerged, they were reared on eggs of the Mediterranean flour moth (*E. kuehniella*) (obtained from Insect Ecology Management Laboratory in the Department of Plant Protection, Ferdowsi University of Mashhad, Iran) and kept for three generations to be used in the experiments. The *T. brassicae* adults were maintained in glass vials (16×100 mm) with hosts. Cultures of *E. kuehniella* and the parasitoid

were kept in an incubator at $23 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH, and 16:8 h L:D photoperiod.

Functional Response

To study the functional response of *T. brassicae*, different egg densities (5, 10, 20, 30, 40, 60, and 80) of *E. kuehniella* were used. Since the cannibalistic larvae of *E. kuehniella* consume parasitized eggs, the eggs were sterilized by deep-freezing at -20°C for 24 hours and then stored at $5 \pm 1^\circ\text{C}$ in a refrigerator. Each host density was prepared by placing a regular dispersion of eggs on a small strip of white card (1.2×6 cm) using 20% diluted honey solution. These densities were separately offered to a single mated female of *T. brassicae* (1-day-old) in a glass vial (16×100 mm) closed with a cotton ball for aeration. Each host density was replicated 20 times. The egg densities were replaced every day until the female died. Their age was expressed as number of days since eclosion.

Data Analysis

Analysis of functional responses data comprises two distinct steps (Messina and Hanks 1998; De Clercq *et al.*, 2000; Juliano, 2001; Mohaghegh *et al.*, 2001; Allahyari *et al.*, 2004). The first step is to determine the type of functional response. Logistic regression analysis [SAS/STAT, CATMOD procedure (SAS version 9.2)] of the proportion of parasitized eggs (N_a) in relation to initial host density (N_0) is the most effective way. The data were fitted by a logistic regression model which describes the relationship between N_a/N_0 and N_0 (Juliano, 1993):

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

Where, P_0 , P_1 , P_2 , and P_3 are the parameters to be estimated. The coefficients in the expression, estimated by fitting the model to the experimental

data on the proportion of N_a/N_0 against N_0 , indicate whether the functional response is of type II or III as the sign of P_1 and P_2 determines the shape of the curves. A positive linear parameter (P_1) indicates that the functional response is type III, whereas a negative linear parameter (P_1) shows that the functional response is type II (Juliano, 1993; Messina and Hanks, 1998).

After determining the type of functional response, the next step is to estimate the handling time (T_h) and searching efficiency (a'). In this study, we used an explicit deterministic

model for type II functional response that was developed concurrently by Royama (1971) and Rogers (1972), called the 'random parasitoid' equation [Equation (2)]:

$$N_a = N_0 \left\{ 1 - \exp \left[- \frac{a' T}{1 + a' T_h N_0} \right] \right\} \quad (2)$$

Where, N_a is the number of parasitized hosts, N_0 is the number of offered hosts, T denotes the total time available for the parasitoid, a' is the searching efficiency, and T_h is the handling time. For a type III response, a' is assumed to increase with host density according to the equation $a' = (d + bN_0)/(1 + cN_0)$ (Hassell *et al.*, 1977). In cases where both d and c are not significantly different from 0, this leads to $a' = bN_0$ which can be inserted into Equation (2). This yields the following (Hassell, 1978):

$$N_a = N_0 \left[1 - \exp \left(- \frac{b T N_0}{1 + b T_h N_0^2} \right) \right] \quad (3)$$

Then, for each host density the attack coefficient (a') could be found as $a' = bN_0$.

An iterative nonlinear least-squares regression (SAS Institute, 2001) was used to fit the random parasitoid equation to data so as to estimate the parameters describing the type II response. Likewise, a non-linear least square regression procedure was used to fit Equation (3) to data producing a type III response. Curves were drawn by Excel.



RESULTS

The three-dimensional plot shows the mean numbers of hosts parasitized against the age of the parasitoid and host density (Figure 1). It is obvious that the mean number of parasitized eggs tended to decrease with parasitoid age, and to increase with host density.

The outcome of logistic regression analysis of the proportion of hosts parasitized by female adults of *T. brassicae* at different ages is presented in Table 1. It shows that the functional response of a female parasitoid is type III during her first day as adult (Figure 2-a). This suggests that parasitism acts as a positive density-dependent mortality factor at low host densities and as a negative density-dependent factor at higher host densities (Figure 2-b). The negative sign of the linear terms ($P_1 < 0$) for the next 8 days reveals that the functional response changed from type III to type II during the remaining part of a female's life. This means that the functional response increased with host density but with a steadily decreasing slope (Figure 3-a), whereas the percentage of parasitism steadily declined (Figure 3-b).

Estimated searching efficiency and handling time at different female ages are shown in Table 2. The regression analysis showed that searching efficiency (a') declined significantly with the age of parasitoid ($F = 7.867$, $df = 2, 5$, $P = 0.026$) (Figure 4-a). In contrast, the handling time increased significantly with age ($F = 46.644$, $df = 1, 7$, $P = 0.0002$) (Figure 4-b). The maximum rate of parasitism (T/T_h) showed a significantly declining trend with age ($F = 17.323$, $df = 1, 7$, $P = 0.004$) (Figure 4-c).

DISCUSSION

To determine the efficiency of a parasitoid in regulating a pest population, the functional response may contain useful information (Hassell *et al.*, 1977; Hassell, 1978). Previous works only studied the functional response of *Trichogramma* species in a 24 hour period experiment. Our study is the first to reveal the functional response of *T. brassicae* to varying densities of *E. kuehniella* at different ages during a parasitoid's life. It may provide us with a better insight into the effective use of this organism in insect pest management. The study shows that the age of *T. brassicae*

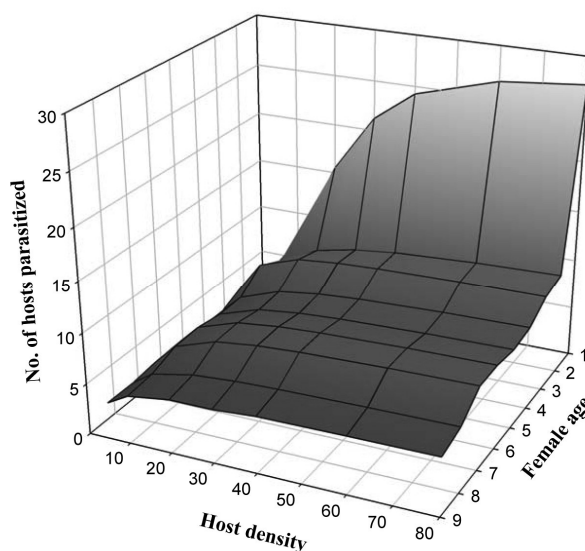
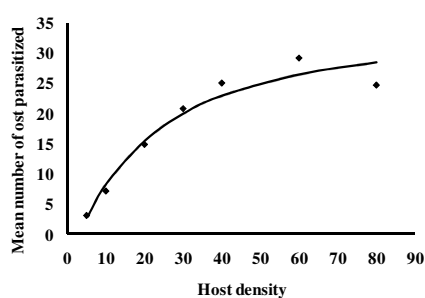


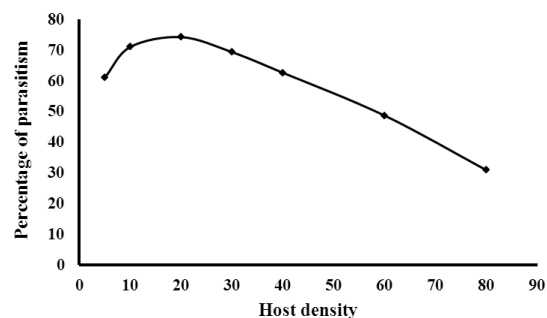
Figure 1. Three dimensional plot showing the effect of the age of *Trichogramma brassicae* and *Ephestia kuehniella* density on mean number of hosts parasitized.

Table 1. Results of the analysis of the maximum likelihood estimates for linear coefficient (P_1) of the logistic model of the proportion of *Ephestia kuehniella* eggs parasitized by *Trichogramma brassicae* adults as a function of initial host density at different ages of life.

Female age (Days)	Parameter	Estimate	SE	X ²	P
1	Constant	0.5236	0.2285	5.25	0.0220
	Linear	0.0431	0.0188	5.26	0.0218
	Quadratic	-0.00132	0.000425	8.54	0.0035
	Qubic	7.203E-6	3.204E-6	5.05	0.0246
2	Constant	0.6520	0.2325	7.86	0.0050
	Linear	-0.0352	0.0205	2.95	0.00734
	Quadratic	-0.00058	0.000523	1.25	0.2630
	Qubic	7.936E-6	3.855E-6	4.24	0.0395
3	Constant	1.2838	0.2483	26.73	0.0001
	Linear	-0.0681	0.0217	9.86	0.0017
	Quadratic	0.000104	0.000549	0.04	0.8497
	Qubic	2.724E-6	4.041E-6	0.45	0.5002
4	Constant	1.1506	0.2558	2.23	0.0001
	Linear	-0.1218	0.0226	29.04	0.0001
	Quadratic	0.00196	0.000573	11.73	0.0006
	Qubic	-0.00001	4.234E-6	8.50	0.0035
5	Constant	1.2670	0.2810	20.34	0.0001
	Linear	-0.1246	0.0244	26.17	0.0001
	Quadratic	0.00175	0.000611	8.20	0.0042
	Qubic	-9.2E-6	4.478E-6	4.22	0.0399
6	Constant	1.3451	0.2958	20.68	0.0001
	Linear	-0.1191	0.0254	21.94	0.0001
	Quadratic	0.00162	0.000636	6.48	0.0109
	Qubic	-8.68E-6	4.659E-6	3.47	0.0624
7	Constant	0.4735	0.2978	2.53	0.1118
	Linear	-0.0352	0.0256	18.47	0.0002
	Quadratic	-0.00048	0.000650	0.54	0.4623
	Qubic	6.065E-6	4.816E-6	1.58	0.2095
8	Constant	0.5742	0.3439	2.79	0.0950
	Linear	-0.582	0.0299	3.79	0.0500
	Quadratic	-0.00031	0.000762	0.16	0.6873
	Qubic	7.307E-6	5.656E-6	1.67	0.1964
9	Constant	0.3173	0.4013	0.63	0.4291
	Linear	-0.0469	0.0341	18.9	0.0006
	Quadratic	-0.00033	0.000870	0.15	0.7009
	Qubic	5.274E-6	6.512E-6	0.66	0.4180



(a)



(b)

Figure 2. Type III functional response (a) and percentage of parasitism (b) at the age of 1 day old *Trichogramma brassicae* female to varying density of *Ephestia kuehniella* eggs.

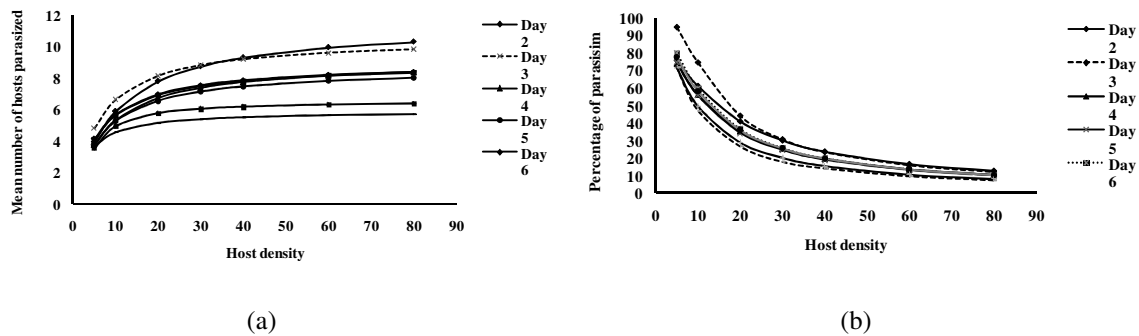


Figure 3. Type II functional response (a) and percentage of parasitism (b) at the ages of 2 to 9 days of *Trichogramma brassicae* female to varying density of *Ephestia kuehniella* eggs.

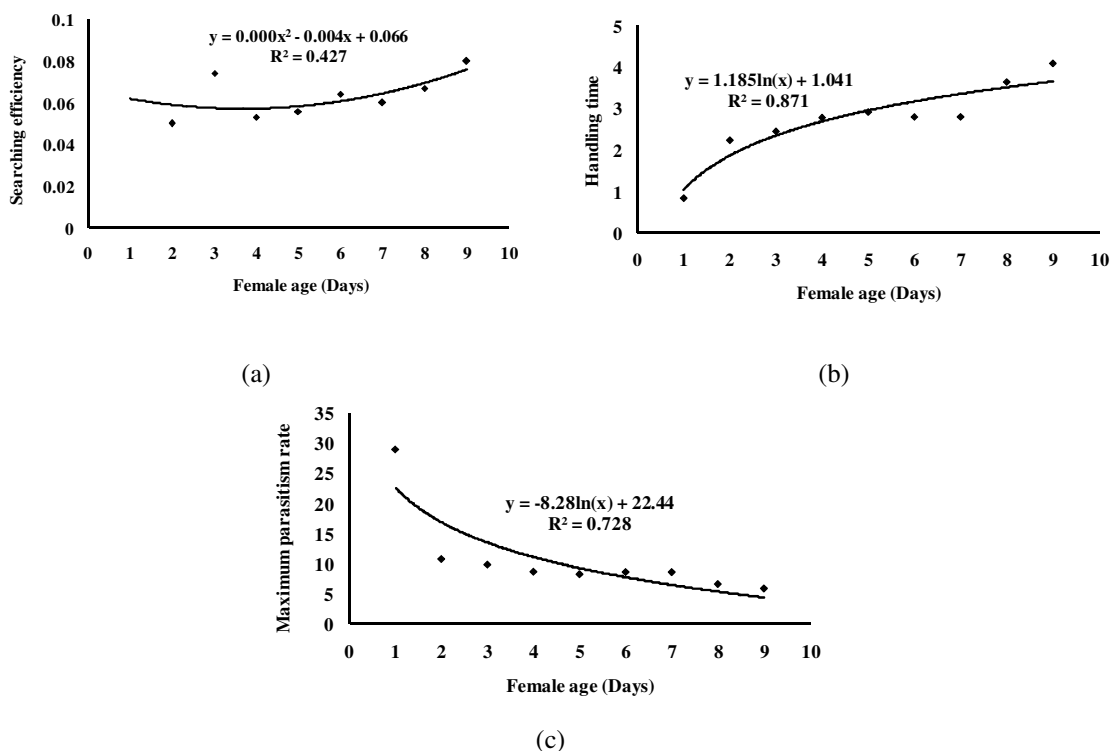


Figure 4. Age-specific searching efficiency (a), handling time (b) and maximum parasitism rate (c) of *Trichogramma brassicae* adults to varying density of *Ephestia kuehniella* eggs.

influences the type of functional response and some relevant aspects of its behavior, such as searching efficiency and handling time, determining its performance as a control agent. So far, few scientists have studied the influence of ageing on the type of functional response in insect natural enemies. However, a linear relationship was reported between the age of *Rhynocoris marginatus* F. (Hemiptera: Reduviidae) (Ambrose et al., 1996). Ding-Xu et al.

(2007) found that the type of functional response by *Scolothrips takahashii* Priesner (Thysanoptera: Thripidae) on *Tetranychus viennensis* Zacher (Acarina: Tetranychidae) eggs differed depending on the sex and the age of adult predator. Furthermore, results from age-specific functional response experiments with *Psyllaephagus zdeneki* (Hymenoptera: Encyrtidae), parasitizing *Euphyllura pakistanica* (Hemiptera: Psyllidae) revealed that the type of

Table 2. Estimated functional response parameters for the female adults of *Trichogramma brassicae* at different ages of life.

Female age (days)	Type	Parameter	Estimate	SE	CI 95%	
					Lower	Upper
1	III ^a	<i>b</i>	0.0037	0.00069	0.0025	0.00491
		<i>T_h</i> (h)	0.831	0.0356	0.7612	0.902
2	II	<i>a'</i>	0.050	0.015	0.020	0.079
		<i>T_h</i>	2.078	0.199	1.684	2.472
3	II	<i>a'</i>	0.074	0.025	0.024	0.125
		<i>T_h</i>	2.272	0.191	1.892	2.652
4	II	<i>a'</i>	0.053	0.018	0.016	0.090
		<i>T_h</i>	2.620	0.244	2.135	3.106
5	II	<i>a'</i>	0.056	0.021	0.013	0.098
		<i>T_h</i>	2.758	0.256	2.249	3.267
6	II	<i>a'</i>	0.064	0.031	0.002	0.126
		<i>T_h</i>	2.659	0.291	2.079	3.239
7	II	<i>a'</i>	0.063	0.028	0.006	0.120
		<i>T_h</i>	2.677	0.278	2.123	3.231
8	II	<i>a'</i>	0.067	0.043	0.020	0.154
		<i>T_h</i>	3.529	0.416	2.700	4.358
9	II	<i>a'</i>	0.083	0.085	0.070	0.255
		<i>T_h</i>	4.037	0.558	2.921	5.152

^aThe value of $a' = bN_0$ in type III response ranged from 0.0185 to 0.296 h⁻¹ at different host densities (5, 10, 20, 30, 40, 60 and 80).

functional response was not affected by parasitoid age (Asadi *et al.*, 2012).

A sigmoid type III functional response was seen during the first day of *T. brassicae*'s adult life, showing an initial increase in the rate of parasitism, followed by a constant rate and then a deceleration of the response as in the type II model. Most hymenopteran parasitoids, especially Trichogrammatidae, exhibit either the type III in a 24 hour period experiment (ArbabTafti *et al.*, 2004; Farazmand and Iranipour, 2006; Reay-Jones *et al.*, 2006; Moezipour *et al.*, 2008), which is in agreement with our finding for one-day-old female, or a type II functional response (Reay-Jones *et al.*, 2006; Moezipour *et al.*, 2008; Farrokhi *et al.*, 2010) as seen when *T. brassicae* became older. It seems that the female parasitoids are highly energetic and efficient during early life only.

Many factors affect searching efficiency and handling time of parasitoids including their age (Sahragard, 1989; Asadi *et al.*,

2012), density (Tahriri *et al.*, 2007), and strain (Farrokhi *et al.*, 2010), as well as host age and density (Chen *et al.*, 2006; Chong and Oetting, 2006a), host developmental stages (González-Hernández *et al.*, 2005; Chong and Oetting, 2006b), temperature and relative humidity (Parajulee *et al.*, 2006; Shojaei *et al.*, 2006; Ding-Xu *et al.*, 2007; Atlihan and Chi, 2008; Moezipour *et al.*, 2008). Relationship between functional response and parasitoid age could be explained by a comprehensive model implicating that both handling time and attack rate are affected by aging. It is an obvious expectation that high rate of parasitism in a parasitoid's early days of life will cause energy loss in aged wasps and may force the female to spend more time on other activities. Thus, we expect the wasps to spend a larger part of time with non-searching activities e.g. resting or feeding, at older ages, while searching and oviposition activities are most prominent during the younger ones (Asadi *et al.*, 2012).



Our results show that the attack rate or searching efficiency showed variability and that handling time increased as female parasitoids aged. These findings are somehow in agreement with similar studies (Ding-Xu *et al.*, 2007; Asadi *et al.*, 2012).

The handling time (time for resting, preening and sap feeding in parasitoids) is a good indicator of the parasitism rate (Atlihan and Guldal, 2009). In our study, the maximum rate of parasitism (T/T_h) decreased as the parasitoid aged, because handling time (T_h) increased with parasitoid age. It has been stated that the asymptote is determined by either the handling time (T_h) (Hassell, 1978), egg limitation or egg retention of female parasitoids (Hassell, 1982; Hassell and Waage, 1984; Reznik *et al.*, 2003). Reznik *et al.* (2003) suggest that the stability of the parasitism is dependent on endocrine system and refusal to oviposit may be considered a specific state which is not controlled by oogenesis, and oviposition behavior is subject to neurohormonal regulation.

In conclusion, this study has improved our knowledge on *T. brassicae*-*E. kuehniella* interactions in the laboratory and has illustrated the potential capacity of *T. brassicae* as an efficient biological control agent to suppress lepidopteran pests as shown by its different types of functional response during its lifetime. It is assumed that parasitoids showing a type III functional response have better opportunities to regulate their host populations than type II parasitoids have, but, in the case of *T. brassicae* both responses occur depending on a female's age. However, the success and failure of a natural enemy in biological control cannot be attributed only to its functional response. Other characteristics such as a short handling time and a tendency to aggregate in areas where hosts are common, a high intrinsic rate of natural increase, as well as host traits, biotic and abiotic factors, plant variety or plant species by physically and biochemically features or indirect influence on host diet, may influence the behavioral aspects and

efficiency of natural enemies (Hassell, 1978; Price, 1986; Jamshidnia *et al.*, 2010).

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واکنش تابعی وابسته به سن *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) با پارازیت‌ها *Ephestia kuehniella* (Lepidoptera: Pyralidae) های مختلف تخم *Ephestia*

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چکیده

زنبر پارازیتوئید *Trichogramma brassicae* Bezdenko در برنامه های کنترل بیولوژیکی علیه بال پولک داران آفت در اکوسیستم های کشاورزی مورد استفاده قرار می گیرد. واکنش تابعی وابسته به سن *T. brassicae* در تراکم های مختلف (۵، ۱۰، ۲۰، ۳۰، ۴۰، ۶۰ و ۸۰) از تخم های عقیم شده بید آرد *Ephestia kuehniella* در شرایط 23 ± 1 درجه سانتی گراد، نم نسبی 60 ± 5 درصد و نسبت روشنایی به تاریکی ۸:۱۶ مطالعه شد. تراکم های تخم *E. kuehniella* به طور جداگانه در اختیار



یک عدد زنبور ماده یک روزه جفت گیری کرده *T. brassicae* قرار گرفتند. تراکم‌های تخم روزانه تا زمان مرگ زنبور جایگزین شدند. آزمایش در ۲۰ تکرار انجام شد. برای روز اول عمر زنبور *T. brassicae* واکنش تابعی نوع سوم و برای زنبورهای ۲ تا ۹ روزه واکنش تابعی از نوع دوم به دست آمد. نتایج تاثیر سن زنبور را روی قدرت جستجو (\hat{a}) و زمان دستیابی (T_h) نشان می‌دهند. با افزایش سن زنبور پارازیتوئید، روند کاهش در قدرت جستجو مشاهده شد. در مقابل، زمان دستیابی زنبور پارازیتوئید با افزایش سن میزبان افزایش نشان داد. کمترین و بیشترین مقدار آن به ترتیب مربوط به روزهای اول و نهم زندگی زنبور بود. همچنین بیشترین نرخ پارازیتیسیم (T/T_h) به طور معنی داری با افزایش سن زنبور کاهش یافت. از این مطالعه می‌توان نتیجه گرفت که ماده‌های زنبور پارازیتوئید *T. brassicae* در روزهای اول عمر خود ممکن است بسیار کارا تر عمل کنند و به طور موثر قادر به کاهش جمعیت پروانه‌های آفت باشند.