Age-specific functional response of *Psyllaephagus zdeneki* (Hymenoptera: Encyrtidae), parasitoid of *Euphyllura pakistanica* (Hemiptera: Psyllidae)

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Abstract: This study was conducted to evaluate the age-specific functional response of *Psyllaephagus zdeneki* Noyes & Fallahzadeh (Hymenoptera: Encyrtidae) at different nymph densities of olive psyllid, *Euphyllura pakistanica* Loginova (Hemiptera: Psyllidae). Due to parasitoid behaviour of feeding and parasitizing the host, both traits were separately explored on a daily functional response. Results of logistic regression revealed a type II functional response of the wasp independent of their ages. The handling time (T_h) and searching efficiency (*a*) were estimated using the Rogers equation. The highest searching efficiency for both parasitism and feeding was observed in the first five days of the adult age. The handling time for parasitism and host feeding increased with the age of female wasp. The highest searching efficiency and shortest handling time for host attacked (Parasitism and feeding) were gained in day 5 and day 2 and maximum parasitism and host feeding in days 2 and 3 of adult female age, respectively. We conclude that *P. zdeneki* demonstrated a reasonable performance as a potential biocontrol agent by feeding and parasitism of *E. pakistanica* which gained its maximum efficiency within 2 to 5 days of its life.

Keywords: *Psyllaephagus zdeneki*, functional response, *Euphyllura pakistanica*

Introduction

Olive psyllid, *Euphyllura pakistanica* Loginova (Hemiptera: Psyllidae) is one of the most important pests of olive orchards in the Fars province of Iran (Asadi *et al.*, 2009a). This pest also has been reported to be present in Pakistan, India and Syria (Loginova, 1972; Thakur *et al.*, 1989; Thakur *et al.*, 1997) and causes economic damage in olive orchards in India (Virender *et al.* 2007). *Psyllaephagus zdeneki* Noyes & Fallahzadeh (Hymenoptera: Encyrtidae) has been described and reported as a new endoparasitoid of *E. pakistanica* for the first time by Noyes and Fallahzadeh (2005) from Fars province of Iran. This parasitoid is active in spring, late summer and autumn and is distributed throughout the entire olive orchards in Fars province (Asadi *et al.*, 2009b).

Study of parasitoid foraging behavior is needed in order to understand how parasitoid affects host population and parasitoid its fitness (reproductive success) in a given environment (van Alphen and Jervis, 1996; Wajnberg *et al.*, 2008). Some theoretical

studies have tried to explain complexities of host-parasitoid relationships including host searching efficiency, patch time allocation and egg maturation strategy ,which are affected by host population or parasitoid size (Ellers and Jervis, 2003; Tenhumberg *et al.*, 2006; Bernstein and Jervis, 2008; van Alphen and Bernstein, 2008). Many scientists who have worked in the field of applied ecology and biological control of agricultural pests have sought to understand different aspects of host-parasitoid relationships such as functional response of parasitoid to host population, variation in parasitoid searching efficiency with female age and the effect of host feeding behavior on the population dynamics of hosts and parasitoids (Hassell *et al.*, 1977; Bellows and Hassell, 1988; Kidd and Jervis, 1989). A substantial number of adult parasitoids feed on their hosts, a behavior known as host feeding strategy and plays an important role in the fitness of a given parasitoid (Jervis and Kidd, 1986; Kidd and Jervis, 1989; Bernstein and Jervis, 2008). The host feeding trait is a strategy which is confined to syn-ovigenic parasitoids and is a very common behaviour among this group of parasitoids. Kidd and Jervis (1989) estimated that about one-third of the world's parasitoid fauna is comprised of host-feeding species. Study of host feeding behaviour in an endoparasitoid wasp, *Psyllaephagus pistaciae* Ferrière revealed a substantial mortality of the pistachio psylla, *Agonoscena pistaciae* Burckhardt and Lauterer (Hemiptera: Psylloidea) by this behaviour (Mehrnejad and Copland, 2006). Most studies of host-parasitoid interactions assume that the number of hosts parasitized per unit of time depends on host density and searching efficiency of parasitoid (Hassell and May, 1973). When a female parasitoid encounters a host, she may lay an egg, and thus invest in her current reproduction, or feed on the host to invest in her future reproduction. Costs and benefits of host feeding will affect the optimal female decision (Bernstein and Jervis, 2008).

In-spite of the evidence on benefits and implications of host feeding on host parasitoid populations, there is a lack of data on the host feeding associated costs (Rivero and West, 2005).

Another important aspect for evaluating the efficiency of a natural enemy is the attack rate and foraging behaviour across a range of host densities, *i.e.*, its functional response (Berryman, 1999). In other words, functional response is a way to assess the impact of natural enemy on a host population (Lester and Harmsen, 2002). A fundamental approach in the way to translate the effect of foraging behaviour on population dynamics by functional response models (Solomon, 1949; Holling, 1959b). Functional response may be used to determine if a natural enemy is able to regulate the density of its host when the response depends on density (Murdoch and Oaten, 1975). Functional response describes the way in which a natural enemy responds to a changing density of its prey and it is a commonly measured attribute of natural enemies (Holling, 1959b; Juliano, 2001). The term functional response was originally coined by Solomon (1949) to describe basic components of the relationship between a natural enemy and its host. In quantifying host-parasitoid interactions functional response is an essential starting point. Holling (1959a) developed a simple model called "disc equation" in which he derived the expected number of prey eaten as a non-linear function of initial constant prey number and the available time. This model assumes sampling with replacement, however Rogers (1972) and Rogers and Hassell (1974) developed another model in which they derived a corresponding equation for sampling without replacement. With the type II response, the numbers of host attacked per parasitoid increases with an initial increase in prey density, but at a decelerating rate toward a plateau. With the type III response, the rate of attack increases at first increases with

increasing prey density, but then decreases, so that the functional response curve is sigmoid (Oaten and Murdoch, 1975; Luck, 1985). The type II and III functional responses are common among arthropod predators (Hassell *et al.*, 1977) and parasitoids (Hassell *et al.*, 1977; Van Lenteren and Bakker, 1978; Chong and Oetting, 2006). The analyses of functional response of the parasitoids is often used to determine the potential effects of parasitoids on host population dynamics (Oaten and Murdoch, 1975).

To our knowledge, no data have been published in the literature concerning the functional response of *P. zdeneki*, a potential biological control agent of olive psyllid. This study was therefore aimed to determine the effect of female age on functional response of *P. zdeneki* at varying densities of *E. pakistanica* to provide basic information for using this potential biological control agent for control of this pest in olive orchards. This information will contribute to better understanding of the role of *P. zdeneki* in suppression of olive psyllid populations and may open a window in developing a biological control program for this pest.

Materials and Methods

Rearing methods and experimental conditions
The populations of olive psyllid, *E. pakistanica* and its parasitoid, *P. zdeneki* were collected from the olive orchards in Shiraz, Fars province of Iran, in autumn 2008. The olive psyllid was reared at 20 ± 1°C and 60 ± 5% relative humidity climate room with a photoperiod of 16:8 (L : D) h. The parasitoid wasps were cultured on olive seedlings infested with *E. pakistanica* in transparent cylindrical cages (25 × 60 cm). Colonies of olive psyllid and its parasitoid were restocked with field collected individuals in late summer and fall in order to prevent any inbreeding effects. The olive psyllid and its parasitoid used in this study were maintained in the laboratory and reared for two generations before using in the experiments.

Functional response study
The effect of host density on parasitism and host feeding was determined during adult life. A pair (male and female) of newly emerged adult of *P. zdeneki* was transferred into rearing containers at seven host density levels (2, 4, 8, 16, 32, 64, 120) of the fourth instar nymphs of *E. pakistamica*. Each treatment (host density) was repeated eight times. The rearing containers in each treatment consisted of a fresh olive offshoot (twig) (7 cm in length) placed on some moistened cotton in a plastic Petri dish (12 × 4 cm). The third and fourth instar nymphs of *E. pakistanica* are suitable for both feeding and parasitism, with no significant differences between them as shown in our previous study (Asadi *et al.*, 2009b). Therefore, the experiments were conducted with fourth instar nymphs. For each density, a pair (male-female) of newly emerged *P. zdeneki* was transferred into each rearing container for 24 h. The parasitoids were then removed from the Petri dishes, and the psyllids were kept in climate room (20 ± 1°C, 60 ± 5٪ RH and 16:8 (L : D) h. The number of dead hosts resulting from feeding was counted every day for three days and mummies for 15 days by stereo-microscope.

Statistical analysis
To determine the type of functional response, the data from each host density in female wasp lifetime for hosts parasitized and hosts attacked (parasitized + eaten) were fitted to a logistic regression analysis for maximum likelihood (SAS Institute, 1999) as suggested by Juliano (2001):

$$\frac{N_a}{N_o} = \frac{\exp(P_o + P_1 N_o + P_2 N_o{}^2 + P_3 N_o{}^3)}{1 + \exp(P_o + P_1 N_o + P_2 N_o{}^2 + P_3 N_o{}^3)}$$

where N_a is the number of psyllid nymphs which is parasitized or eaten, N_o is the number of hosts available and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively. Significant negative or positive linear coefficients (*i.e.*, P_1) indicate functional response type II or III, respectively. The slope of the type II response is declining (*i.e.*, P_1 is negative), whereas that of the type III response is accelerating (*i.e.*, P_1 is positive).

Then the handling time (T_h) and searching efficiency (a') were estimated using a type II equation for parasitoids (Rogers 1972):

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

where N_a is the number of hosts parasitized and number of hosts attacked (parasitized + eaten), N_o is the number of hosts available, a' is the searching efficiency, T is the whole time of the experiment (24 h.), T_h is the period of time which elapsed from the encountering the host to the end of parasitism or feeding per host (*i.e.*, handling time) and P_t is the number of parasitoids. The maximum number of hosts parasitized and hosts attacked were calculated by dividing total time (24 h) by T_h. The functional response parameters were estimated using nonlinear least squares regression. Statistical analysis of functional response was performed using SAS statistical software (SAS Institute 2003).

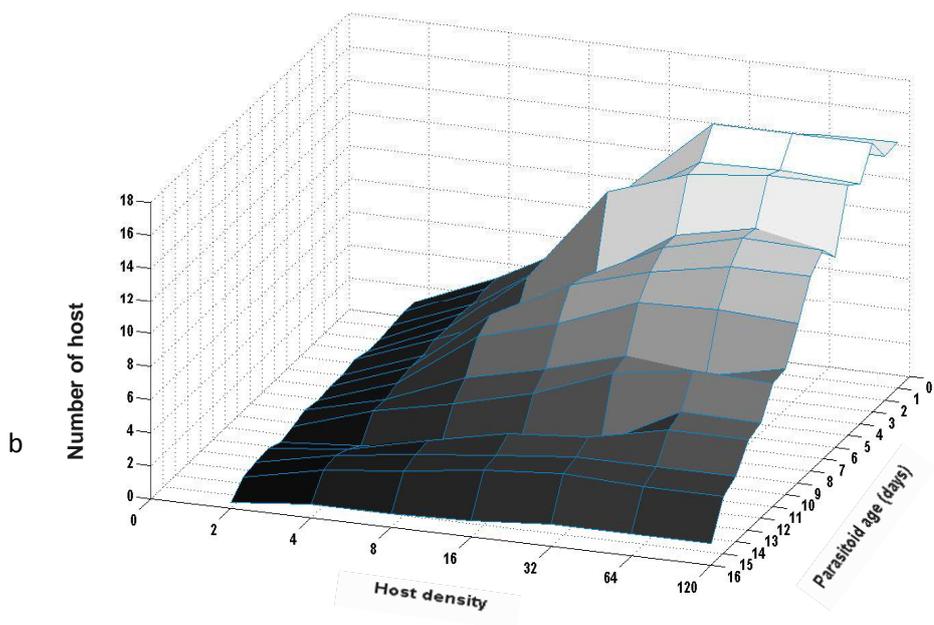Mean number of hosts attacked (parasitism and host feeding) at different host densities were analyzed using one-way ANOVA. If significant differences were detected, multiple comparisons were made using the Student-Newman-Keuls (SNK) at $P < 0.05$.

Results

The relationship between mean number of hosts parasitized and hosts attacked with the age of parasitoid and host density are illustrated in Fig. 1. Mean number of host parasitized and attacked at each density decreased with increasing parasitoid life time. For example, the mean number of host parasitized at the density of 120 nymphs, was estimated at 13.50, 9.25 and 0.66 in the first, eight and 16th day of adult female age, respectively. Mean numbers of host attacked at the density of 120 nymphs also showed a decline rate with parasitoid age, which were estimated to be 15.00, 11.87 and 1.33 in the first, 8th and 16th day of adult female age, respectively. Also the mean number of parasitism and host attacked increased with host density in the whole parasitoid lifetime. For example, the mean numbers of host parasitized on the first day of adult female age at the density of 2, 4, 8, 16, 32, 64 and 120 were estimated to be 1.12, 2.62, 5.62, 10.50, 12.87, 13.25 and 13.50, respectively. The regression analyses between mean number of hosts parasitized with host density at each parasitoid age were related positively in the first ($R^2 = 0.97$), 8th ($R^2 = 0.99$) and 16th day ($R^2 = 0.96$) of adult female age. In contrast regression analyses between total number of hosts attacked with the host density the estimated equations are: ($y = 3.62\ln(x)-0.33$, $R^2 = 0.96$) in the first, ($Y = 2.61\ln(x)-0.93$, $R^2 = 0.93$) in the eight and ($y = 0.23\ln(x)-0.36$, $R^2 = 0.94$) in the 16th day of adult female age.
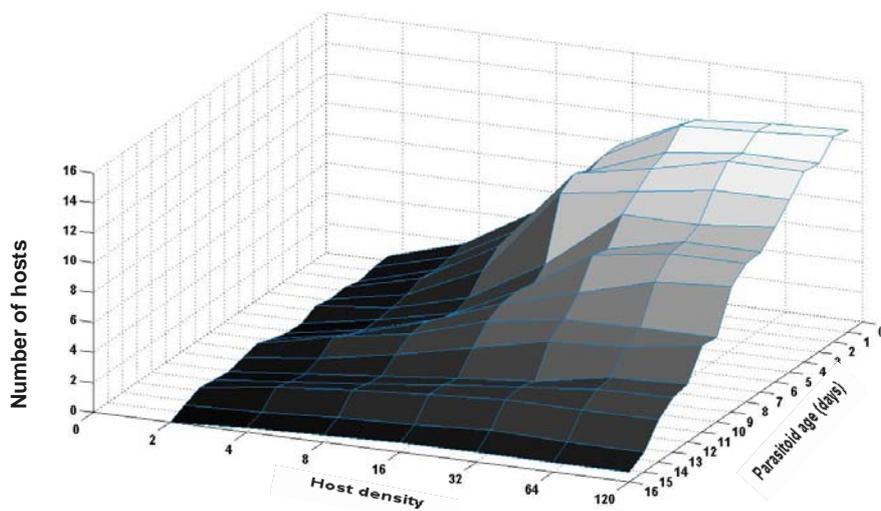
a

b

Figure 1 Three-dimensional contour plot showing the effect of the age of *Psyllaephagus zdeneki* and *E. pakistanica* density on mean number of hosts parasitized (a) and total number of hosts attacked (b).

Data fitted to a logistic regression showed significant negative linear coefficient (i.e. P_1) for hosts parasitized and hosts attacked which indicated a type II functional response (Table 1). Type of functional response was not affected by parasitoid female age. Mean numbers of parasitized and attacked nymphs, as predicted by Rogers model at various parasitoid female ages are plotted and illustrated in Fig. 2. Both attack rate and parasitization rate decreased with the host density and the age of parasitoid.
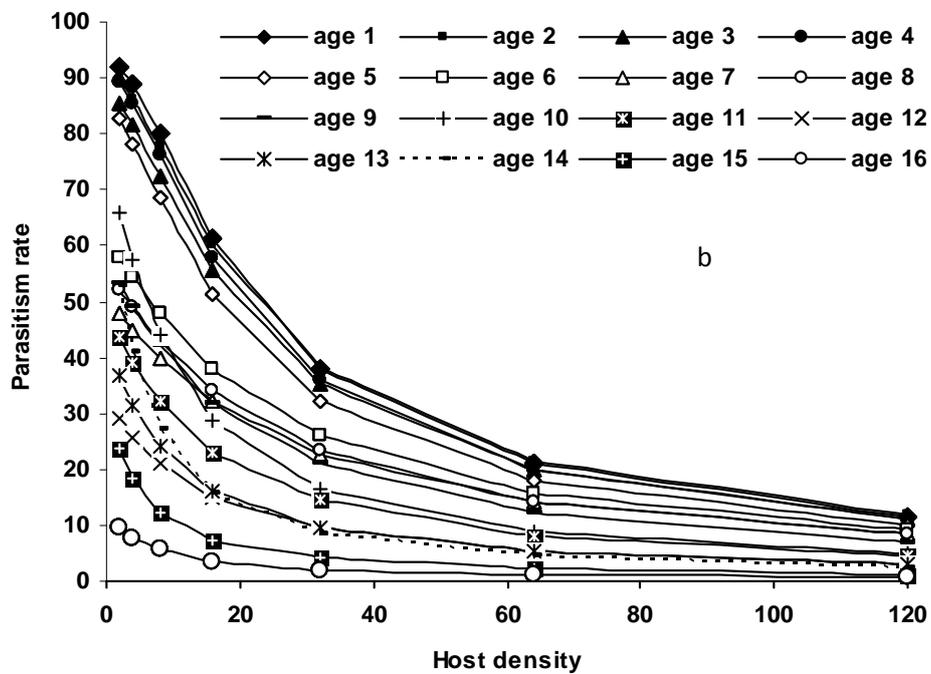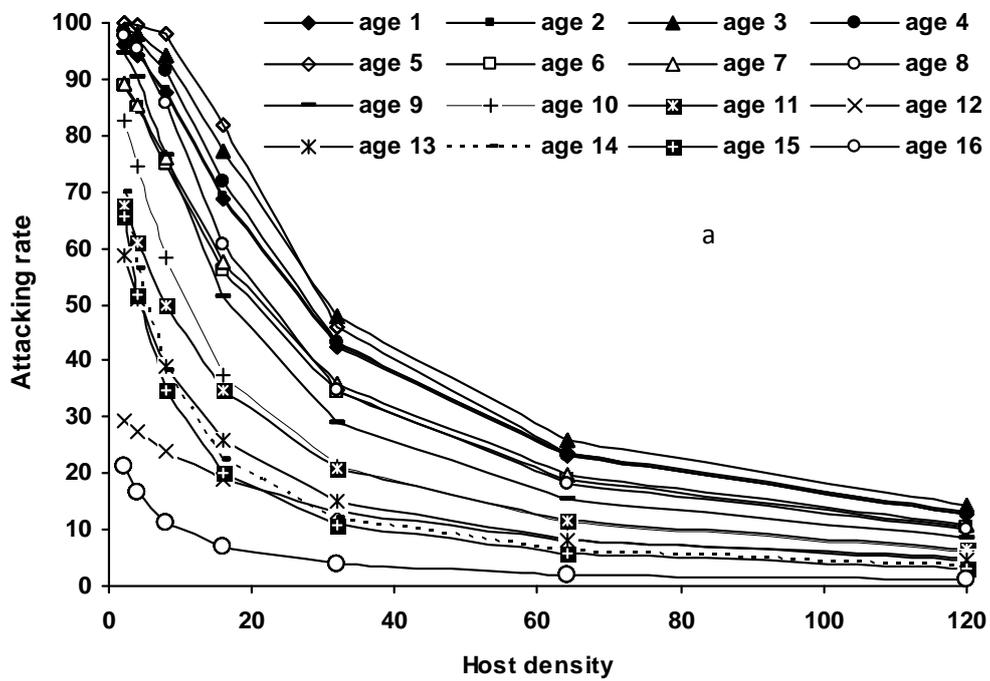
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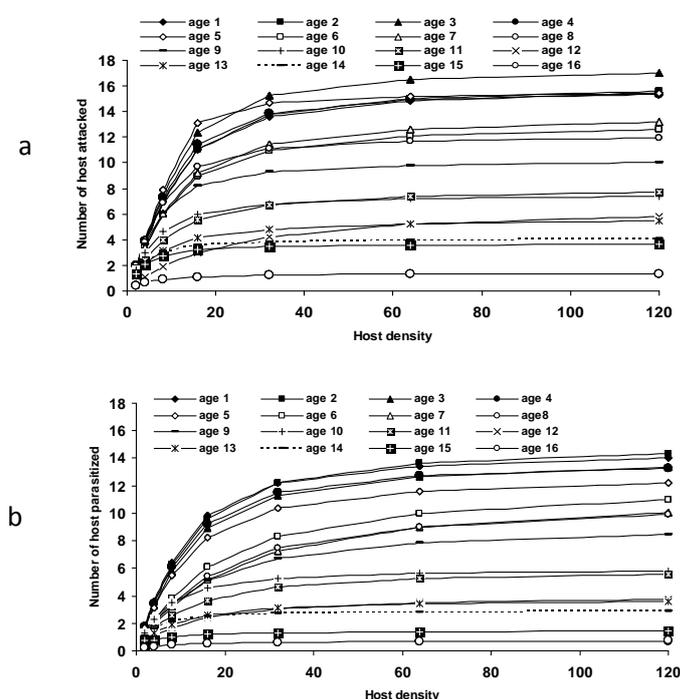
Figure 2 Age specific functional response (attacking: a, parasitism: b) of *P. zdeneki* at different densities of *E. pakistanica* using Rogers type II model.

Table 1 Results of the analysis of the maximum likelihood estimates for linear coefficient (P_1) of the logistic model to fit the data of *Psyllaephagus zdeneki* to the selected functional response type on adult female life time.

Female parasitoid age (days)	linear coefficient (P_1) (mean ± SEM)	
	Hosts parasitized	**Hosts attacked**
1	-0.0448 ± 0.0218	-0.1338 ± 0.0265
2	-0.0205 ± 0.0116	-0.1166 ± 0.0261
3	-0.0108 ± 0.0114	-0.1040 ± 0.0266
4	-0.0365 ± 0.0118	-0.1005 ± 0.0254
5	-0.0128 ± 0.0115	-0.1667 ± 0.0307
6	-0.0114 ± 0.0021	-0.1220 ± 0.0242
7	-0.0077 ± 0.0032	-0.1056 ± 0.0237
8	-0.0053 ± 0.0029	-0.1546 ± 0.0262
9	-0.0613 ± 0.0234	-0.1296 ± 0.0245
10	-0.1004 ± 0.0247	-0.1210 ± 0.0244
11	-0.0742 ± 0.0258	-0.1123 ± 0.0240
12	-0.0982 ± 0.0302	-0.1211 ± 0.0277
13	-0.0987 ± 0.0293	-0.1242 ± 0.0258
14	-0.1195 ± 0.0342	-0.1337 ± 0.0312
15	-0.0856 ± 0.0455	-0.1222 ± 0.0317
16	-0.0434 ± 0.0254	-0.0939 ± 0.0476

Mean numbers of nymphs parasitized at different ages of parasitoid showed significant differences (F = 5.25, df = 15, 120, P < 0.001). Mean numbers of host attacked also differed significantly at different ages of parasitoid (F = 4.51, df = 15, 120, p < 0.001). The highest proportion of host attacked was observed during the first five days of the parasitoid female age and a substantial percentage of the hosts were attacked by parasitoid in the first week of female age (Fig. 3). The very important effect of host feeding on the percentage of hosts attacked is considerable especially in the first week of adult female age (Fig. 3).

Rogers' type II equation was fitted for two conditions in parasitoid female lifetime in order to determine and compare the searching efficiency and handling time at different female ages. The estimated values of searching efficiency and handling time of these two traits in *P. zdeneki* lifetime are shown in Table 2.

Figure 3 Percentage of the age specific functional response (attacking: a, parasitism: b) of *P. zdeneki* on different densities of *E. pakistanica*.

Table 2 Estimated values for searching efficiency (a') and handling time (T_h) from Rogers' type II equation for *Psyllaephagus zdeneki* females of different ages search rate, handling time and maximum value of coefficient of determination (R^2) in adult female life time.
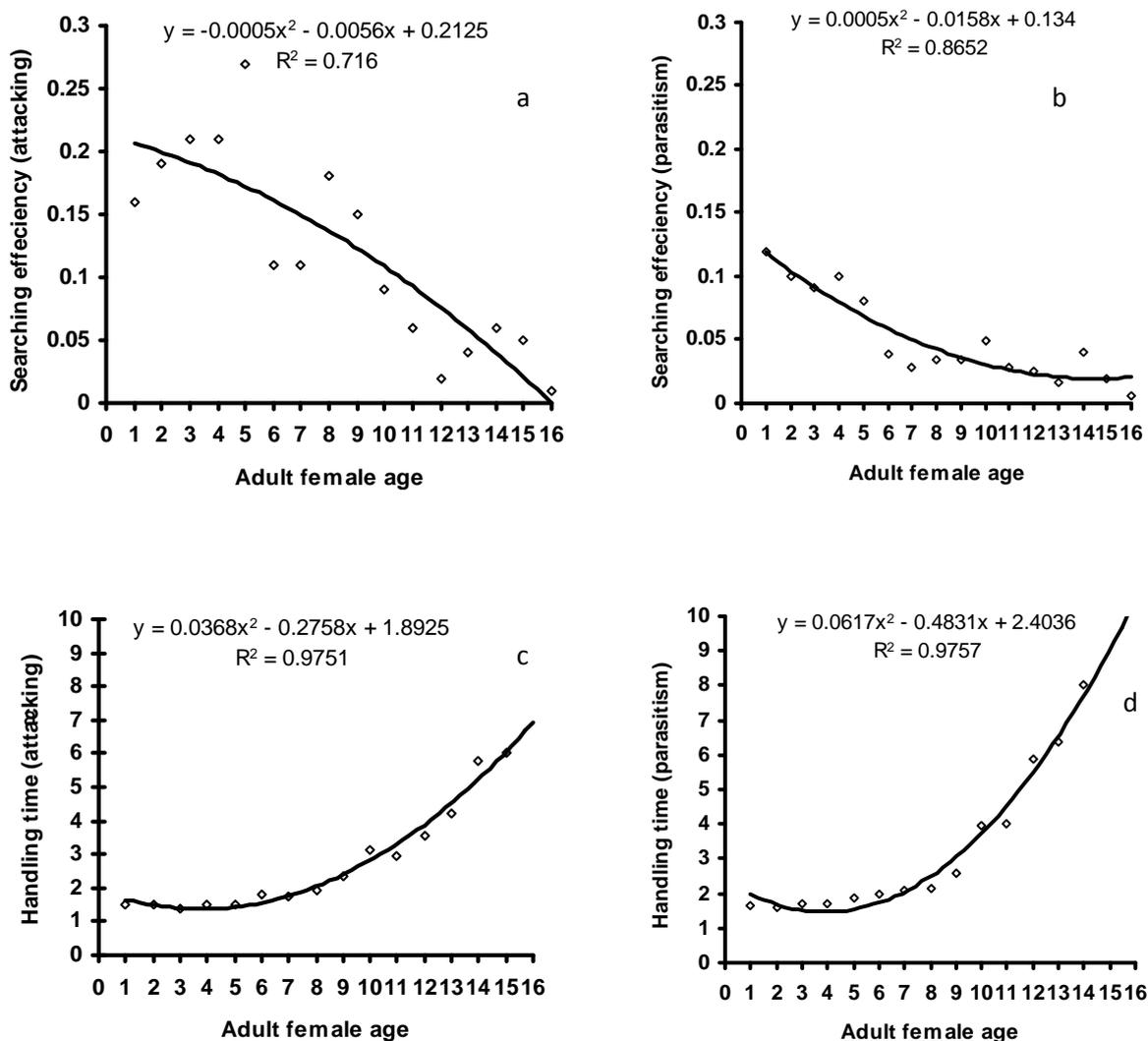
| Female parasitoid age (days) | No. of Hosts parasitized | | | Maximum number of hosts parasitized | No. of Hosts attacked | | | Maximum number of hosts attacked |
	Searching efficiency (h^{-1})	Handling time (h^{-1})	R^2		Searching efficiency (h^{-1})	Handling time (h^{-1})	R^2	
1	0.12 ± 0.03	1.64 ± 0.08	0.90	13.63	0.15 ± 0.03	1.50 ± 0.05	0.92	16
2	0.11 ± 0.03	1.59 ± 0.08	0.87	15.1	0.16 ± 0.04	1.48 ± 0.06	0.86	16.22
3	0.09 ± 0.02	1.70 ± 0.09	0.83	14.12	0.21 ± 0.06	1.36 ± 0.05	0.88	17.65
4	0.11 ± 0.03	1.73 ± 0.10	0.93	13.87	0.21 ± 0.06	1.51 ± 0.07	0.95	15.89
5	0.08 ± 0.02	1.87 ± 0.09	0.82	12.83	0.28 ± 0.02	1.53 ± 0.06	0.85	15.69
6	0.04 ± 0.02	1.97 ± 0.14	0.78	12.18	0.11 ± 0.02	1.82 ± 0.08	0.81	13.17
7	0.03 ± 0.006	2.10 ± 0.16	0.79	11.43	0.11 ± 0.01	1.73 ± 0.05	0.91	13.12
8	0.03 ± 0.008	2.17 ± 0.18	0.75	11.06	0.18 ± 0.06	1.95 ± 0.09	0.78	12.31
9	0.04 ± 0.007	2.59 ± 0.19	0.77	9.27	0.15 ± 0.03	2.34 ± 0.08	0.84	10.26
10	0.06 ± 0.020	3.9 ± 0.32	0.73	6.05	0.09 ± 0.01	3.15 ± 0.19	0.79	7.62
11	0.03 ± 0.009	3.99 ± 0.39	0.70	6.02	0.06 ± 0.02	2.97 ± 0.26	0.66	8.08
12	0.02 ± 0.005	5.89 ± 0.56	0.69	4.01	0.03 ± 0.01	3.57 ± 0.39	0.62	6.72
13	0.02 ± 0.009	6.35 ± 0.83	0.67	3.78	0.05 ± 0.01	4.21 ± 0.31	0.64	5.70
14	0.05 ± 0.029	8.11 ± 0.42	0.64	2.96	0.08 ± 0.03	5.78 ± 0.42	0.60	4.15
15	0.02 ± 0.009	16.40 ± 2.95	0.60	1.46	0.07 ± 0.002	6.05 ± 0.81	0.61	3.97

Regression analysis showed significant relationship between searching efficiency (a') and handling time (T_h) with the age of female parasitoid (Fig. 4). The highest searching efficiency (a') was gained in the first day of parasitoid life for host parasitism (0.12±0.03 h^{-1}) and the fourth day for hosts attacked. Nevertheless, the highest value for a' was

estimated to be in the first five days of adult female life. The *a´* value for hosts parasitized declined with the age of parasitoid but when we assumed searching for host attacked to include

both parasitism and host feeding in Rogers model, this value showed slight fluctuations in adult female lifetime: ascending in first few days and then gradually declining (Fig. 4a, b).

$$y = -0.0005x^2 - 0.0056x + 0.2125$$
$$R^2 = 0.716$$

$$y = 0.0005x^2 - 0.0158x + 0.134$$
$$R^2 = 0.8652$$

$$y = 0.0368x^2 - 0.2758x + 1.8925$$
$$R^2 = 0.9751$$

$$y = 0.0617x^2 - 0.4831x + 2.4036$$
$$R^2 = 0.9757$$

Figure 4 Age-specific searching efficiency (attacking and parasitism) and handling time of *P. zdeneki* on fourth instar nymphs of *E. pakistanica*.

Handling time, the time which was spent for parasitism or host feeding by *P. zdeneki* showed an increasing trend by adult female age in both traits (Table 3). The lowest value of handling time in parasitism was gained for one and two

days old females (Fig. 4d). In combined handling time for traits: parasitism and host feeding, a slight decreasing trend was observed from the day one (1.4985 ± 0.0492) to the day three (1.3695 ± 0.0559) of the parasitoid age

then gradually increased with the age of parasitoid. The trends of handling time in different ages of parasitoid in combined (host feeding and parasitism) (Fig. 4c) with the data on parasitism (Fig. 4d), it is clear that host feeding behaviour reduced the overall handling time which is seen in figures by comparing the slope of two curves. Decreasing parasitism by the age of parasitoid also resulted in steep slope of the curve and lengthening of handling time from the second week of the parasitoid age.

Discussion

Our results demonstrated a prominent role for the parasitoid, *P. zdeneki* in reducing the host, *E. pakistanica* population in laboratory which unveiled potential capability of the parasitoid as an effective biological agent. *P. zdeneki* caused a reasonable mortality of the host by parasitism of 15.1 host nymphs and attacking (parasitism and feeding) 17.65 hosts in a period of 24 h. Parasitoid exhibited a very efficient perform-ance in the first week of its life with high parasitism and host feeding. Our findings also revealed the fundamental role of the parasitoid age and host feeding on the functional response of *P. zdeneki*. Results of this study demonstrate how handling time may play a considerable role in efficient performance of parasitoids, which is neglected in many studies. This is the first study on the functional response of *P. zdeneki* on *E. pakistanica* which opens a window on using this organism in biological control programs of olive psyllid.

The effectiveness of a parasitoid in regulating a pest population has been tradition-ally referred to as its functional response (Hassell, 1978). The negative values for the linear parameters (P_1) gained in the present study confirmed the type II functional response for parasitoid at all ages. Most hymenopteran parasitoids especially Encyrtidae family studied exhibit either type II (González-Hernández *et al*. 2005; Matadha *et al*., 2005; Sagarra *et al*., 2000; Chong and Oeting, 2006) which is in agreement with our finding, or a type III functional response (Jones *et al*. 2003; Sagarra

et al., 2000). Van Lenteren and Bakker (1978) suggested that the rarity of the type III model in functional response studies may be the result of an experimental artifact. In this manner the type II model is the most common observed model for parasitoids, especially in experim-ental condition when parasitoids are kept in captivity and caged with their hosts in a small arena for a fixed period of time and potentially report of type II function in this study may have suffered from the same weakness. A type II functional response with decelerating parasitism rate has a potential to destabilize host-parasitoid dynamics due to inverse density-dependent host mortality which may stabilize the host population dynamics (Murdoch and Oaten 1975; Luck, 1985). The Rogers random attack equation adequately described the increase in the numbers of host attacked (Parasitism and feeding) by *P. zdeneki* with increasing host density at all ages. *P. zdeneki*, attack rate is similar to that in *Anagyrus* sp. nr. *sinope* and also in *Anagyrus ananatis* Gahan (Hymeno-ptera: Encyrtidae) (González-Hernández *et al*., 2005; Chong and Oeting, 2006). In this study we determined that the maximum number of *E. pakistanica* nymphs were attacked by three days old *P. zdeneki*; 17.65 hosts per day and considerably higher than other encyrtids like *Anagyrus* sp. nr. *sinope* (Hymenoptera: Encyrtidae) which parasitized 13.3 nymphs of *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae) per day as described by Chong and Oetting (2007). The effect of parasitoid age on functional response could be described by an extended model indicating that parasitoid age affects both instantaneous attack rate and handling time (of the parasitoid), which has been somewhat neglected in many functional response studies. This reveals that the parasitoid will spend a long time with non-searching activities (*e.g.*, resting) at older ages, while more searching, oviposition and predatory activities would be expected at younger ages. We tried to include this information in our result to rectify this weakness. Results of Age-specific attack rates revealed the highest attack rate of *P. zdeneki* on the host *E. pakistanica*

during the initial 6 days post adult emergence. This finding is supported by previous studies of two other encyrtid *A. ananatis* and *Clausenia josefi* (Rosen) which parasitized the greatest percentage of available hosts during the first 6 and 4 days of their adult lives, respectively (González-Hernández *et al*. 2005; Berlinger 1973). Also the estimated handling times of *P. zdeneki* were close to those reported by Chong and Oeting (2007) for an encyrtid parasitoid, *Anagyrus* sp. nr. *sinope* (0.85h to 1.8h in different host stages). It is essential to obtain actual handling time through behavioral experiments because according to Chen *et al.* (2006), the handling times were overestimated in Rogers (1972) model because the experimental period (24h) was longer than the actual time period when the parasitoids were active (16h light). Hymenopteran parasitoids show positive phototaxis and are active only during the light period (Stary, 1970). It is an obvious expectation that handling time increase by changing condition.

Host feeding is an important behavioral trait among syn-ovigenic parasitoid species as a major means to obtaining proteins for egg production (Jervis and kidd, 1986; Heimpel *et al.*, 1996; Thompson, 1999; Bernstein and Jervis, 2008). This behavioral characteristic of parasitoids has been gravely neglected (Yamamura and Yano, 1988). Host feeding affects parasitoids key life-history variables like fecundity and longevity and plays a major role in their fitness as reviewed by Bernstein and Jervis (2008). Neglecting host feeding behavior of parasitoids may result in a serious misunderstanding of host-parasitoid population dynamics, since many parasitoids kill significant numbers of hosts by feeding as well as by parasitism (Kidd and Jervis 1989). The time that parasitoids devote to different activities during their lifetime is shared between various functions such as consumption of food resources, searching for host and activities linked with parasitism. Time allocation between these activities is one of the most important dilemmas in decision making by adult parasitoid to gain maximum fitness (Bernstein and Jervis, 2008).

The effect of host feeding in increasing the instantaneous attack rate and also decreasing the overall handling time has been demonstrated for this parasitoid in the present study. Our previous study exhibited the destructive non-concurrent feeding behaviour of *P. zdeneki* which caused a considerable impact on host population (Asadi *et al.*, 2009b). This type of host-feeding has been reported specially by an encyrtid, *P. pistaciae* (Mehrnejad and Copland, 2006) and some other hymenopteran parasitoids (Heimpel *et al.*, 1996; Lampson *et al.*, 1996). The host death resulting from the host feeding may be caused by a direct effect of feeding or indirect feeding behaviours like injection of the venom by the parasitoid and its probing activities (Kidd and Jervis, 1989). *P. zdeneki* exhibited a relatively high range of mortality on different psyllid nymphal instars by both host feeding and parasitism which is very important in biological control programs. According to our earlier study all five psyllid nymphal instars were susceptible to parasitism by *P. zdeneki* but the third and fourth psyllid instar nymphs were more frequently preferred for parasitism than the others. Host feeding by *P. zdeneki* is an important behaviour causing the death of a substantial number of the first and second nymphal instars of the host (Asadi *et al.*, 2009b). As the experimental conditions were based on the preferred stages for parasitism which caused a biased condition toward parasitism rather than host feeding. In natural conditions, however, where different nymphal stages are present the contribution of host feeding in increasing the parasitoids attack rate is more likely.

The results on searching rate estimates for *P. zdeneki* exhibited an overall higher range in younger females than in older ones. This suggests that *P. zdeneki* could feed on and parasitize more of *E. pakistanica* nymphs in the first five days of its lifetime. The ability of *P. zdeneki* to find, feed and parasitize *E. pakistanica* over its lifetime with reasonable attack rate provides the opportunity to introduce this parasitoid as a good candidate for biological control program of olive psyllid in

Iran, where the psyllid and parasitoid exist from April to November in most olive orchards of Fars province (Asadi, 2010). The results of laboratory study supported the capability of *P. zdeneki* in using this parasitoid in biological control programs of olive psyllid. Functional response studies in small laboratory areas have been criticized as being unrepresentative of natural conditions (Kareiva 1990). However, the success and failure of a natural enemy in biological control can not be attributed only to functional response. Other factors such as intrinsic rate of natural increase, host traits, biotic and abiotic factors have a major influence on the efficiency of natural enemies, in addition to tritophic and intraguild interactions (Jamshidnia *et al.*, 2010). To conclude we suggest additional laboratory and field studies are required to determine the effect of different factors on functional response of *P. zdeneki* to establish basic information in using this organism in biological control program of olive psyllid in Iran.

Acknowledgments

References

Asadi, R., Talebi, A. A., Burckhardt, D., Khalghani, J., Fathipour, Y., and Moharramipour, S. 2009a. On the identify of the olive psyllids in Iran (Hemiptera, Psylloidea). Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 82:197-200.

Asadi, R., Talebi, A. A., Khalghani, J., Fathipour, Y., and Moharramipour, S. 2009b. Host stage preference of *Psyllaephagus zdeneki* (Hymenoptera: Encyrtidae), a parasitoid of *Euphyllura pakistanica* (Hemiptera: Psyllidae) in Iran. The 5th International Iran and Russia Conference on Agricultural Sciences. pp. 106-108.

Asadi, R. 2010. Bioecology of olive psyllid, *Euphyllura pakistanica* (Hemiptera: Psyllidae) and its parasitoids *Psylaephagus zdeneki* (Hymenoptera: Encyrtidae) in Fars province. PhD dissertation, Tarbiat Modares University, Tehran.

Bellows, T. S., and Hassell M. P. 1988. The dynamics of age-structured host-parasitoid interactions. Journal of Animal Ecology, **57:**259-268.

Berlinger, M. J. 1973. Biological studies of *Clausenia josefi* (Hym. Encyrtidae), a parasite of *Planococcus vitis*. Entomophaga, 18: 279-286.

Bernstein, C. and Jervis, M. A. 2008. Food-searching in parasitoids: the dilemma of choosing between 'immediate' or future fitness gains. In: Wajnberg E, van Alphen JJM, (Eds.) *Behavioural Ecology of Parasitoids*. Oxford: Blackwell.

Berryman, A. A. 1999. The theoretical foundations of biological control. In: Hawkins B.A., Cornell, H. V. (Eds.). *Theoretical approaches to biological control*. Cambridge University Press, Cambridge. pp. 3-21.

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

Chong, J. H., and Oetting, R. D. 2006. Functional response and progeny production of the Maderia mealybug parasitoid, *Anagyrus* sp. nov. nr. sinope: the effects of host and parasitoid densities. Biological Control, 39: 320-328.

Chong, J. H., and Oetting, R. D. 2007. Functional response and progeny production of the Maderia mealybug parasitoid, *Anagyrus* sp. nov. nr. sinope: the effects of host stage preference. Biological Control, 41: 78-85.

Ellers, J. and Jervis, M. A. 2003. Body size and the timing of reproduction in parasitoid wasps: habitat-dependent allocation strategies. Oikos, 102**,** 164-172.

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

Hassell, M. P., and May, R. M. 1973. Stability in insect host-parasite models. Journal of Animal Ecology, 42: 693-726.

Hassell, M. P., Lawton, J. H., and Beddington, J. R. 1977. Sigmoid functional response by invertebrate predators and parasitoids. Journal of Animimal Ecology, 46:249-262.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, N. J.

Heimpel, G. E., Rosenheim J.A., and Mangel M. 1996. Egg limitation, host quality, and dynamic behaviour by a parasitoid in the field. Ecology, 77: 2410-2420.

Holling C. S. 1959a. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. The Canadian Entomologist, 91: 293-320.

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

Jamshidnia, A., Kharazi-Pakdel, A., Allahyari, H., Soleymannejadian, E. 2010. Functional response of *Telenomus busseolae* (Hym.: Scelionidae) an egg parasitoid of the sugarcane stem borer, *Sesamia nonagrioides* (Lep.: Noctuidae) at different temperatures. Biocontrol Science and Technology, 20: 631-640.

Jervis, M. A., and Kidd, N. A. C. (1986). Host-feeding strategies in hymenopteran parasitoids. Biological Reviews of the Cambridge Philosophical Society, 61: 395-434.

Jones, D. B., Giles K. L., Berberet, R. C., Royer T. A., Elliott, N. C., and Payton M. E. 2003. Functional responses of an introduced parasitoid and an indigenous parasitoid on greenbug at four temperatures. Environmental Entomology, 32: 425-432.

Juliano, S. A. 2001. Nonlinear curve-fitting: predation and functional response curves. In: Scheiner, S. M., Gurevitch, J. (Eds.) Design and analysis of ecological experiments. 2nd edition, Oxford University Press, New York, pp. 178-196.

Kareiva, P. 1990. The spatial dimension in pest-enemy interaction. In: Mackauer, M., Ehler, L.E., Roland, J., (Eds.), Critical Issues in Biological Control, Intercept. Anover, Hants, pp. 213-227.

Kidd, N. A. C., and Jervis, M. A. 1989. The effects of host feeding behaviour on the dynamics of parasitoid-host interactions, and the implications for biological control. Researches on Population Ecology, 31: 235-274.

Lampson, L. J., Morse, J. G., and Luck, R. F. 1996. Host selection, sex allocation, and host feeding by *Metaphycus helvolus* (Hymenoptera, Encyrtidae) on *Saissetia oleae* (Homoptera, Coccidae) and its effect on parasitoid size, sex, and quality. Environmental Entomology, 52: 283-294.

Lester, P. J., and Harmsen, R. 2002. Functional and numerical responses do not always indicate the most effective predator for biological control: An analysis of two predator in a two-prey system. Journal of Applied Ecology, 39: 455_468.

Loginova, M. M. 1972. On the fauna of Psylloidea (Homoptera) from Morocco. Commentationes Biologicae. 37 pp.

Luck, R. F. 1985. Principles of arthropod predation. In: Huffaker, C.B., Rabb, R.L. (Eds.), Ecological Entomology. Wiley, New York, PP. 497-530.

Matadha, D., Hamilton, G. C., Lashomb J. H., and Zhang, J. 2005. Ovipositional prefere-nces and functional response of parasitoids of euonymous scale, *Unapis euonymi* (Comstock) and San jose scale, *Quadraspid-iotus perniciosus* (Comstock) (Homoptera: Diaspididae). Biological Control, 32: 337-347.

Mehrnejad, M.R. and Copland, M. J. W. 2006. Host-stage selection and oviposition behaveiour of *Psyllaephagus pistaciae*, paras-itoid of the common pistachio psylla, *Agonoscena pistaciae*. Biological Control, 36: 139-146.

Murdoch, W. W., and Oaten, A. 1975. Predation and population stability. Advances in Ecological Research, 9: 1-131.

Noyes, J. S., and Fallazadeh, M. 2005. *Psylalephagus zdeneki* sp. nov. (Hymenoptera: Encyrtidae) form Iran, parasitoid of *Euphyllura pakistanica* (Hemiptera: Psyllidae). Acta Societatis Zoologicae Bohemicae, 69: 203-208.

Oaten, A., and Murdoch, W. W. 1975. Functional response and stability in predator-prey systems. The American Naturalist, 109: 289-298.

Rivero, A., and West, S. A. 2005. The costs and benefits of host feeding in parasitoids. Animal Behaviour, 69: 1293-1301.

Rogers, D. J. 1972. Random search and insect population models. Journal of Animal Ecology, 41: 369-383.

Rogers, D. J., and Hassell, M. P. 1974. General models for insect parasite and predator searching behaviour: interference. Journal of Animal Ecology, 43: 239-253.

Sagarra, L. A., Vincent, C., Peters, N. F., and Stewart, R. K. 2000. Effect of host density, temperature and photoperiod on the fitness of *Anagyrus kamali*, a parasitoid of the hibiscus mealybug *Maconellicoccus hirsutus*. Entomologia Experimentalis et Applicata, 96: 141-147.

SAS Institute 1999. SAS user's guide, version 8.2. SAS Institute, Cary, NC,USA.

SAS Institute 2003. JMP: a guide to statistical and data analysis, version 5.0.1. SAS Institute, Cary, NC.

Solomon, M. E. 1949. The natural control of animal populations. Journal of Animal Eology, 18: 1-35.

Stary, P. 1970. Biology of aphid parasites (Hymenoptera: Aphidiidae) with respect to integrated control. Dr. W Junk N.V., The Hague.

Tenhumberg, B., Siekmann, G. and Keller, M. A. (2006). Optimal time allocation inparasitic wasps searching for hosts and food. Oikos, 113: 121-131.

Thakur, J. R., Sharma and Gupta, P. R. 1989. Occurrence of olive psylla, *Euphyllura pakistanica* Loginova (Homoptera: Aphalar-idae) on olive in India: A new record. International Journal of Pest Management, 25 (3): 331.

Thakur, J. R., Atwal, R. K., and Gupta, P. R. 1997. Insect pests of olive in Himachal Pradesh. Pest management and Economic Entomology. Pest Management and Economic Zoology, 5: 75–79.

Thompson, S. N. 1999. Nutrition and culture of entomophagous insects. Annual Review of Entomology, 44: 561-592.

Van Alphen, J. J. M., and Jervis, M. J. 1996. Foraging Behaviour. In: Jervis M. A., Kidd, N. A. C. (Eds.) Insect Natural Enemies, pp. 1-62. Chapman and Hall, London.

van Alphen, J. J. M. and Bernstein, C. 2008. Information acquisition, information processing, and patch time allocation in insect parasitoids. In: Wajnberg E., van Alphen J. J. M., (Eds.) Behavioural Ecology of Parasitoids. Oxford: Blackwell.

van Lenteren, J. C., and Bakker, K. 1978. Behavioral aspects of the functional response of a parasite (*Pseudeucoila bochei* Weld) to its host (*Drosophila melanogaster*). Netherlands Journal of Entomology, 28: 213-233.

van Lenteren, J. C., Bakker, K., and Van Alphen, J. J. M. 1978. How to analyze host discrimination. Ecological Entomology, 3: 71-75.

Virender, K., Malik, G. H., Uma, S., and Monobrullah, M. 2007. Incidence and management of olive psylla, *Euphyllura pakistanica*. Indian Journal of Entomology, 69: 331–340.

Wajnberg, E., Carlos Bernstein, C. and van Alphen, J. 2008. Behavioural Ecology of Insect Parasitoids: From theoretical approaches to field applications. Wiley-Blackwell.

Yamamura, N., and Yano, E. 1988. A simple model of host-parasitoid interaction with host-feeding. Researches on Population Ecology, 30: 353-369.

واکنش تابعی وابسته به عمر در زنبور (Hymenoptera: Encyrtidae) *Psylaephagus zdeneki* پارازیتویید (Hemiptera: Psyllidae) *Euphyllura pakistanica*

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چکیده: این تحقیق به‌منظور ارزیابی واکنش تابعی وابسته به عمـر در زنبـور پارازیتوییـد *Psyllaephagus zdeneki* Noyes & Fallahzadeh (Hymenoptera: Encyrtidae) روی تراکم‌های مختلف پـوره‌هـای پـسیل زیتون، *Euphyllura pakistanica* Loginova (Hemiptera: Psyllidae) انجام شد. بـه دلیـل داشـتن رفتـار تغذیه از میزبان و پارازیتیسم، هر دو ویژگی رفتاری در قالب واکنش تابعی روزانه مورد بررسی قـرار گرفـت. نتایج رگرسیون لوجیستیک نشان دهنده واکنش تابعی نوع دوم در همه عمر زنبور پارازیتوییـد بـود. زمـان دستیابی و قدرت جستجوی زنبور پارازیتویید با اسـتفاده از معادلـه راجـرز تعیـین شـد. بیـشترین قـدرت جستجو برای پارازیتیسم و تغذیه در پنج روز اول عمر حشرات کامل مـشاهده شـد. زمـان دسـتیابی بـرای پارازیتیسم و تغذیه با افزایش عمر زنبور ماده افـزایش یافـت. بیـشترین قـدرت جـستجو و کمتـرین زمـان دستیابی برای میزبان‌های مورد حمله قرار گرفتـه (پارازیتیـسم و تغذیـه) بـه‌ترتیـب در روز پـنجم و دوم و حداکثر پارازیتیسم و تغذیه به‌ترتیب در روز دوم و سوم عمر حشرات کامل تعیین شد. بر اساس نتـایج بـه‌دست آمده زنبور پارازیتویید *P. zdeneki* از توانایی قابل‌توجهی به‌عنوان عامل کنتـرل بیولوژیـک پـسیل *E. pakistanica* برخوردار است و بیشترین کارایی را در روزهای دوم تا پنجم عمر حشرات کامل دارد.

واژگان کلیدی: *Psyllaephagus zdeneki*، واکنش تابعی، *Euphyllura pakistanica*