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Research Article

Gregarious development alters host utilization by the egg parasitoid *Ooencyrtus fecundus* (Hymenoptera: Encyrtidae)

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Abstract: *Ooencyrtus fecundus* Ferriere and Voegele (Hymenoptera: Encyrtidae) is a gregarious egg parasitoid of sunn pest *Eurygaster integriceps* Puton. Superparasitism enables a female to produce multiple progeny per host and thus reduces the time spent searching for hosts, but results in progressively smaller progeny as more individuals compete for limited resources within hosts. In this study, we tested whether gregarious development would affect the functional response of *O. fecundus* reared under laboratory condition (26 ± 2 ºC, 50 ± 10% RH and 16: 8 L: D h). Various host densities (1, 2, 4, 8, 16 and 32 eggs) were offered to females that had developed either as single, or as twins, triplets or quadruplets within host eggs. To resolve the functional responses of these females, a total exposure time of five hours was chosen, based on direct observations of handling time and the maximum daily number of host attacks/female. Functional response of the parasitoid was type III in singleton and twin parents, and type II in triplet and quadruplet ones. However, host mortality rate was 100% in host densities ≤ 8, suggesting density independence at lower densities as expected from a type I functional response. In such circumstances, handling time is expected to be zero, but was observed to be 11.4 to 14.3 minutes in different treatments. These results suggest that when enough time was available to find and handle all hosts, a type II functional response resembles Type I one. Searching efficiency increased and handling time decreased with body size of the parasitoid of four categories.

Keywords: Hymenoptera, Encyrtidae, *Eurygaster integriceps*, searching ability, functional response

Introduction

Common sunn pest *Eurygaster integriceps* Puton (Hemiptera, Scutelleridae) is one of the most important and well known pests of wheat in Iran and the Middle East. Losses caused by this pest are both quantitative (reduced yields) and qualitative (reduced grain quality). Egg parasitoids are important sources of mortality for sunn pest in wheat fields. One wide spread species is *Ooencyrtus fecundus* Ferriere and Voegele (Hym.: Encyrtidae) (Ferriere, 1961) that was first reported in Iran by Nozadbonab and Iranipour (2010). *O. fecundus* is a gregarious, idiobiont, egg parasitoid of sunn pest, a few other true bugs, and the eggs of some moths. It is also a facultative hyperparasitoid of *Trissolcus* spp. (Hym. Scelionidae). As a gregarious species, it often superparasitizes host eggs; up to nine parasitoid eggs have been reported from a single host egg

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(Safavi, 1970), and a maximum of four wasps can emerge successfully from an egg of *E. integriceps* (Iranipour, 1996; Rafat, 2013).

The functional response of a predator refers to the relationship between prey density and the number attacked. A parasitoid represents a special case in that it consumes only one prey (host) during its life (Hassell, 1978; Rosenbaum and Rall, 2018). The concept was introduced to science by Solomon (1949) and was formalized by Holling (1959; 1966) who used mathematical models to characterize three types of functional response; although now four types have been described (Liu *et al*., 2004). Parameters of predator-prey models such as searching rate and handling time have been used to predict the impact of a natural enemy on a pest (Hassell, 1978; van Alphen and Jervis, 1996; Montoya *et al*., 2000; Xiao and Fadamiro, 2010; Fathipour and Maleknia, 2016). For example, a parasitoid is expected to be more effective in pest control if its parasitism rate is density dependent (Hassell, 1978; Houck and Strauss, 1985; O'Neil, 1990). For this reason, a type III functional response is often considered to be superior for biological control purposes. However, the searching rate is not constant in this type of response and may increase linearly or hyperbolically with host density (Kfir, 1983).

The functional responses of *Trissolcus* spp. egg parasitoids have been studied, but *Ooencyrtus* spp. have not yet been examined in this regard. For example, Fathipour *et al*. (2000) studied the effects of two wheat cultivars, Falat (resistant) and Sardari (susceptible) on the functional response of *Trissolcus grandis* (Thomson) (Hym.: Scelionidae), in both glass tubes and on potted plants and observed a type II functional response on Falat and a type III response on Sardari. The functional response of *T. semistriatus* to *Graphosoma lineatum* L. and *E. integriceps* eggs was type II and III respectively (Asgari *et al*., 2001). On the other hand, Allahyari *et al.* (2004) reported a type III functional response for *T. grandis* on eggs of sunn pest and *Podisus maculiventris* Say. Four species of *Trissolcus* [*T. basalis* (Wollaston), *T. brochymenae* (Ashmead), *T. teretis* Johnson and *T. urichi* (Crowford)], exhibited a type III response to eggs of *Echistus hero* (F.) (Laumann, 2008). *T. djadetshkoe* (Rjachovsky) showed type III response to sunn pest eggs independent of previous experience and insemination or virginity status of female, although virgin and inexperienced females had higher attack rates (Abdi *et al*., 2015). Similarly *T. vassilievi* (Mayr) showed type III response with the same parameter values independent of the parasitoid population origin and in comparison to their intercrossed F1 progeny (Benamolaei *et al*., 2018 a; b).

Superparasitism has long been observed in both field and laboratory studies (Salt 1961, Dorn and Beckage, 2007; Ueno, 2015) and consists of the deposition of two or more eggs into a single host, either by the same female parasitoid, or by a series of conspecifics. In solitary parasitoids, only one larva survives in each superparasitized host, leading to competition among larvae for possession of the host. Competition may take the form of oophagy, physical attacks with special mandibles, or various forms of physiological suppression (Salt, 1961; Fisher, 1963; van Driesche and Bellows, 1996; Vinson and Hegazi, 1998; Köse and Kivan, 2018). Larvae of gregarious parasitoids tolerate one another, but exploitation competition for resources still occurs; larvae may suffer fitness costs such as reduced adult size, prolonged development, reduced fertility and fecundity and other impacts (van Alphen and Visser, 1990; Godfray, 1994; Mackauer and Chow, 2015). Gregarious development may influence the foraging efficiency and functional response of a parasitoid by altering key foraging parameters such as host handling time and rate of parasitism. In this study, we examined how different levels of gregarious development (one, two, three or four larvae per host egg) affect the functional response of *O. fecundus* females.

Materials and Methods

Host rearing

Collections of sunn pest adults were made in January, February and March of 2012 from overwintering sites on Bozkosh Mountain, Ahar County, East Azerbaijan Province, Iran. The insects were held in a greenhouse in the Department of Plant Protection, University of Tabriz. The bugs were housed in rectangular plastic containers (10 × 15 × 30 cm), 40 insects/ container. The bottom of each container was covered with paper, and wheat kernels were supplied as source of food, and water provided on a ball of cotton in a glass dish. Ventilation was provided by a rectangular aperture in the container lid covered with organdy mesh. The containers were maintained in the greenhouse in 25 ± 2 °C, 40 ± 10% RH and photoperiod of 16: 8 (L: D) h. Eggs were collected daily and used in egg traps for collecting parasitoids from wheat fields, for parasitoid rearing, and as hosts in experiments.

Parasitoid rearing

Host egg traps were constructed from rectangular pieces of yellow and green cardboard (5 × 15 cm) folded twice to form a Π shape. Four clutches of host eggs were stuck to the inner surfaces of each trap using odorless glue and each trap was fastened by a thread to wheat plant at a height of 50.0 cm, and spaced approximately 10 m apart. One week later, the traps were removed and brought to the laboratory; eggs with a shiny black appearance indicative of parasitism were held in glass tubes in a growth chamber at 25 ± 2 °C, 50 ± 5% RH and photoperiod of 16:8 (L: D) h until parasitoids emerged. Individuals of *O. fecundus* were selected from among the various species emerging.

Direct observations

To determine the maximum daily attack rate of an individual wasp and total time required, the parasitoid's behavior was directly observed under a stereomicroscope. These observations were then used to estimate maximum host densities and total exposure times in the functional response experiments. Ten 24-48 h-old, mated, but inexperienced, *O. fecundus* females of the F_4 generation were selected at random and four clutches of host eggs (14 ± 1 eggs/clutch) were offered to each female. We then measured the time allocated to the following behaviors for each host egg attacked: probing (contact by the ovipositor with host egg chorion, prior to drilling), piercing (drilling into the host egg with the ovipositor), oviposition (inferred as the quiescent period between piercing and withdrawal of ovipositor), host marking (depositing stem-like structures on host egg with the ovipositor), grooming and the sum of all non-host-associated behaviors (NHA behaviors) including: walking, resting *etc*. The experiment was stopped when a female left the patch and remained outside it for10 minutes.

Functional response experiments

Based on preliminary observations, the total duration of functional response experiments was set at five hours and the highest parasitoid density was set to exceed the maximum number of parasitism events observed. Hence, experiments were comprised of host densities of 1, 2, 4, 8, 16 and 32 eggs with 30, 25, 25, 25, 20 and 15 replications, respectively. To obtain wasps for the experiment, 20 host egg clutches, each consisting of 14 eggs, were offered to 20 female wasps in an arena for 24 h, after which 100 eggs were randomly selected, separated from their clutches, and isolated in glass tubes (1.5 × 10 cm) until emergence. Four different types of wasps were thus obtained: singletons, twins, triplets or quadruplets, according to whether one, two, three or four wasps emerged from a single host egg. Each female was provided with a male of the same type (singleton, twin, triplet or quadruplet) and a drop of honey solution; supernumerary females were removed from all replicates in which they occurred. After 24 h, each experimental female was provided with a specific host density for a period of five hours. The host eggs were then held in a growth chamber at 26 ± 2 °C, 50 ± 10% RH and photoperiod of 16: 8 (L: D) h. The number of parasitized eggs, the gender of emerging wasps, and the time of emergence were all recorded.

Data analysis

To detect whether superparasitism was randomly distributed among host eggs, we tested whether the number of attacks on individual host eggs conformed to a Poison distribution with a mean equal to the mean number of wasps emerging per host egg using Pearson's Chi square test. We further assumed that a maximum of four wasps could emerge from host eggs with ≥ 4 eggs.

Data on the duration of various behaviors obtained from direct observations (i.e., probing, piercing, oviposition, host marking, grooming, and NHA behaviors (defined above) were analyzed by linear regression, plotting them against the host attack sequence. Functional response data were analyzed per Juliano (1993) in two-step model selection using logistic regression in the CATMOD procedure of SAS (SAS Institute, 2011) and parameter estimation using NLIN procedure. The first step led to determination of type II or III functional responses. In type III model searching efficiency (a) is a hyperbolic function of initial density (N_0):

$$\alpha = \frac{d + bN_0}{1 + cN_0} \tag{1}$$

in which b, c, and d, are constants estimated by including observed data; c and d were excluded in two steps when they were not significantly different from zero, a simplification that leads to a decreased form of two-parameter type III functional response with a linear relationship between searching efficiency and initial density:

$$\alpha = bN_0 \tag{2}$$

Results

Superparasitism

The observed pattern of superparasitism was non-random (Table 1); the number of singleton progeny exceeded expectation and all other categories were below expectation, suggesting this wasp tends to avoid superparasitism, but not completely.

Table 1 Incidence of different numbers of *Ooencyrtus fecundus* wasps emerging per host egg compared to expectations of a random (Poisson) distribution.

Entries	No. of emerged wasps per host egg				
	1	2	3	4	Total
Observed	48	23	16	13	100
Expected	32.55	31.58	20.42	15.44	100
Chi-square	7.32	2.33	0.95	0.38	10.99
P	0.028	ns	ns	ns	0.004

Behavioral observations

Female wasps required almost four hours of foraging to completely deplete their daily egg load. The mean duration of behaviors (in minutes) was: probing, 11.11 ± 0.36; piercing, 5.23 ± 0.27; oviposition, 167.0 ± 3.68; host marking, 11.12 ± 0.67; grooming, 10.5 ± 1.13 and NHA behaviors (resting, walking etc.), 19.48 ± 1.44, for a mean total foraging time of 224.46 ± 4.98 minutes. These values correspond to a handling time of 12.71 ± 0.29 minutes per host egg. Based on these observations, five hours were allocated for functional response experiments to ensure no time limitation occurred. An average of 17.5 ± 1.49 host eggs were parasitized, from which a mean of 17.7 ± 1.19 progeny emerged. Maximum daily parasitism was 20 host eggs per wasp, so maximum host density in the functional response experiments was set at 32.

Regression of behavior durations on host attack sequence (from first to last) revealed no significant changes in time spent per host on piercing, oviposition or host marking, the primary behaviors involved in host exploitation (Table 2). However, the duration of other behaviors increased as a function of host attack sequence. The most marked increase was in the time allocated to NHA behaviors, followed by probing and grooming, such that the total time spent per host increased with attack sequence, although not when NHA behaviors were excluded. Thus, increases in time spent per host egg resulted largely from increases in time devoted to NHA behaviors, as reflected in the similarity of line slopes between total time and NHA behaviors. NHA behaviors also exhibited the greatest variation in duration over the course of the experiment, ranging from less than 30 seconds in the first attack to more than two minutes in the last (20th) attack (Fig. 1).

Table 2 Linear regression of the duration of various *Ooencyrtus fecundus* behaviors on host attack sequence.

Behavior	*F*	*P*	Slope
Probing	75.52	< 0.0001	1.13
Piercing	3.58	0.06	0.19
Oviposition	0.01	0.91	-0.16
Host marking	2.70	0.10	0.28
Grooming	15.70	< 0.0001	0.91
NHA behaviors	18.34	< 0.0001	4.93
Total	7.17	0.008	5.27
Total (-NHA behaviors)	2.02	0.15	2.36

Functional response

Parasitism was ca. 100% in all treatments, provided density did not exceed eight host eggs, and at least one adult wasp emerged per host, implying density independent host mortality and a type I functional response (Fig. 2).

The fecundity of *O. fecundus* was 14-20 at the highest host densities and female wasps rarely superparasitized while they had access to unparasitized hosts. Search time was close to zero likely because of the confines of the small vial. Since a total of 254.2 minutes was required to obtain maximum per capita parasitism (*i.e.*, 20 host eggs) and the experiment lasted 300 minutes, females were not time-limited in the experiment. Furthermore, with an effective host density ≤ 14, neither time nor egg load were limiting, so that parasitism reached 100% at densities ≤ 8. At a density of 16 host eggs, the number of progeny produced by triplet and quadruplet wasps was lower than the number of available hosts, with a few host eggs left unparasitized. However, singleton and twin females produced 7-9% more progeny than host eggs available, and also 2.5-3.5% of hosts remained unparasitized. A maximum of 16-18 host eggs were parasitized in different treatments at the highest host density (32 eggs) and superparasitism was very low (≤ 1%).

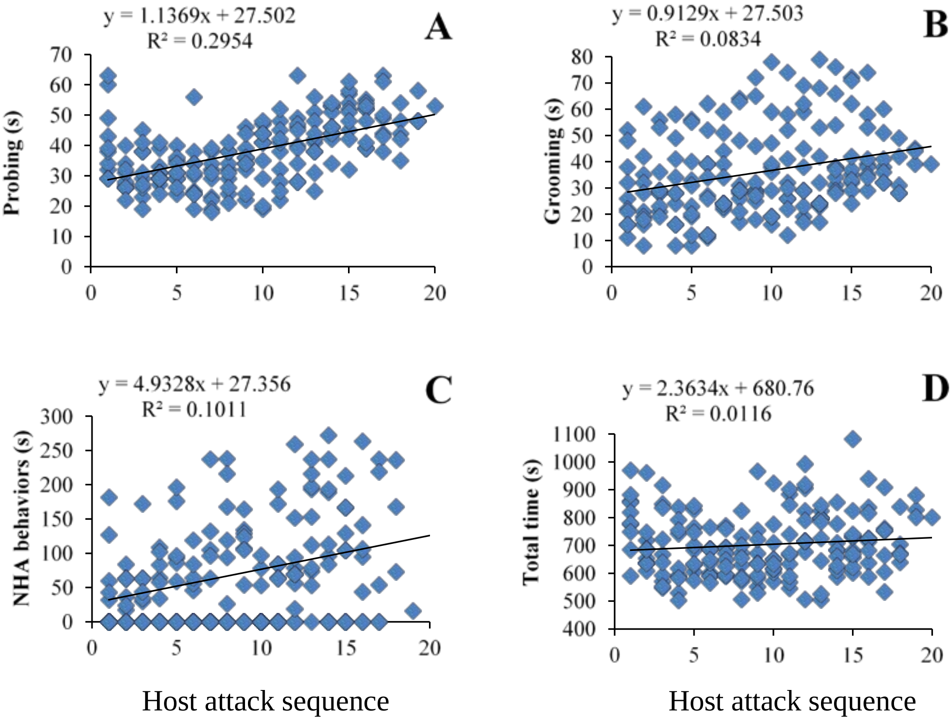

Figure 1 Changes in the duration of various host-associated and non host-associated (NHA) behaviors as a function of host attack sequence: A. Probing, B. Grooming, C.NHA behaviors, D. Total time.

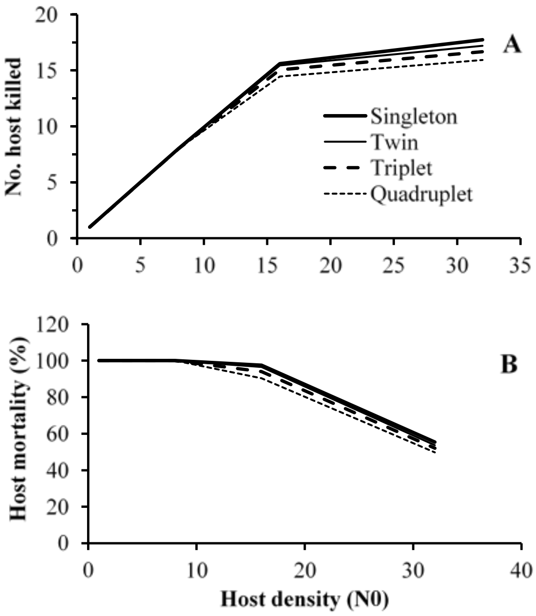

Figure 2 Host mortality caused by *Ooencyrtus fecundus* in different densities of sunn pest eggs A) Number of mortality, B) Percent of mortality.

Percentage of host exploitation was calculated as:

$$\frac{\text{Number of progeny}}{4 \times \text{Number of available host}} \times 100\%$$

At all host densities, the maximum difference of percentage of exploitation was recorded between singletons and quadruplets. At the lowest density the difference was 35%, it reached a maximum of 75% at the density of four host eggs and then gradually reduced at higher densities to reach to less than 12% at the highest density (Fig. 3).

A reduction in the number of progeny /host in densities below four host eggs was observed in singleton and twin parents (Table 3). This is the direct result of competition between wasp larvae. The maximum number of progeny that emerged from an individual host was 2.64 which was recorded in singleton wasps in density of four host eggs. In the same treatment 2.2 progeny emerged in density of one host egg. This may be due to stronger resource waste at lower host density in which competition level is higher. At density of eight host eggs, superparasitism was still considerable (1.4-1.88/ host) but at higher densities a sudden decline occurred, as 1.07 and 1.01 progeny emerged per host on the average in densities 16 and 32 respectively, i.e. ≤ 1% at the highest density.

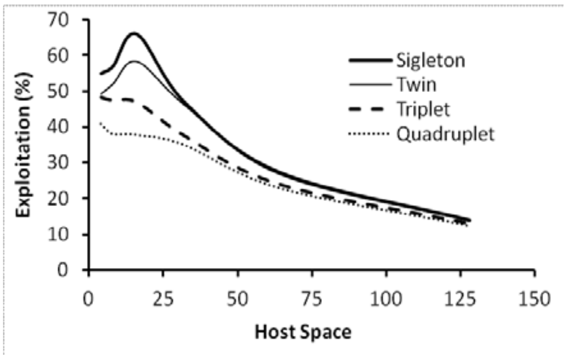

Figure 3 Percent of host exploitation by *Ooencyrtus fecundus* in different densities of *Eurygaster integriceps* eggs.

Taking into account that an individual host egg provides resources for the development of four wasp larvae (Iranipour, 1996; Rafat, 2013), we multiplied each host density by four in the functional response analyses and then analyzed the data. Based on a logistic regression, functional response was determined to be type II, III, II and III for singleton, twin, triplet, and quadruplet wasps respectively. Linear parameter P_1 as well as some other parameters were non-significant in cubic polynomial regression in different analyses and hence a further simplified quadratic model was fitted to the data. The new analysis showed type II functional response in all cases. Data inspection revealed however that the percent of parasitism in singleton and twin wasps has an increasing trend up to the density of four host eggs (16 host carrying capacities for parasitoid); a characteristic type III response in contrast to the results of the logistic regression. High variance of the data is probably a reason. Consequently, parameter estimation was carried out with both type II and III models and error sum of squares (SSE's) were used as criterion to determine type of response. It confirmed a type III response for singleton and twin wasps again (Table 4). Handling time estimations by the two models has somewhat different results (Table 4). Type III model displayed a negative relationship between handling time and body size. On the other hand it was equal in all treatments except twin wasps in type II estimates. The maximum attack rate (T/T_h) also ranged from 16 to 20.5 in different estimates with a general tendency of higher asymptotes in Type II estimates.

Table 3 Average number of *Ooencyrtus fecundus* progeny emerged from available number of *Eurygaster integriceps* eggs (columns Total) and number of progeny per parasitized host (columns Per capita)**.**

Number of hosts	Singleton		Twin		Triplet		Quadruplet		Average	
	Total	Per capita	Total	Per capita	Total	Per capita	Total	Per capita	Total	Per capita
1	2.20	2.20	1.97	1.97	1.93	1.93	1.63	1.63	1.93	1.93
2	4.56	2.28	4.16	2.08	3.80	1.90	3.04	1.52	3.89	1.95
4	10.56	2.64	9.32	2.33	7.52	1.88	6.04	1.51	8.36	2.09
8	15.04	1.88	14.76	1.85	12.04	1.51	11.20	1.40	13.26	1.66
16	17.50	1.12	17.10	1.11	15.40	1.02	14.70	1.02	16.18	1.07
32	17.87	1.01	17.40	1.01	16.80	1.01	16.00	1.00	17.02	1.01

Table 4 Parameter estimates of functional response models in *Ooencyrtus fecundus*. The *a* and *b* are density independent and density dependent searching rates of type II and type III models respectively, T_h and T/Th are handling time and maximum attack rate respectively, SSE is error sum of squares and CL is confidence level of the estimated parameters.

Group	Parameter	Type III Model	Type II Model
Singleton	a or b	0.0010 ± 0.0312	0.3849 ± 0.025
	CL 95%	0.0275 - 0.035	0.3349 - 0.4349
	T_h	0.2804 ± 0.003	0.2430 ± 0.005
	CL 95%	0.2739 - 0.2869	0.2329 - 0.2532
	SSE	223.97	327.19
	T/T_h	17.83	20.57
Twin	a or b	0.0243 ± 0.001	0.2640 ± 0.0178
	CL 95%	0.0213 - 0.0273	0.2288 - 0.2992
	T_h	0.2835 ± 0.003	0.29 ± 0.007
	CL 95%	0.2761 - 0.2908	0.2759 - 0.3041
	SSE	251.41	380.86
	T/T_h	17.63	17.24
Triplet	a or b	0.0153 ± 0.0008	0.2058 ± 0.008
	CL 95%	0.0136 - 0.017	0.1884 - 0.2233
	T_h	0.3073 ± 0.004	0.2461 ± 0.004
	CL 95%	0.2992 - 0.3155	0.2364 - 0.2559
	SSE	197.51	165.87
	T/T_h	16.27	20.31
Quadruplet	a or b	0.0103 ± 0.0006	0.1574 ± 0.008
	CL 95%	0.009 - 0.0115	0.1411 - 0.1737
	T_h	0.3133 ± 0.005	0.2432 ± 0.007
	CL 95%	0.3033 - 0.3232	0.2293 - 0.257
	SSE	231.16	251.42
	T/T_h	15.95	20.55

In triplet and quadruplet wasps, functional response curve reached to a plateau at lower densities (1, 2 and 4 host eggs). This may suggest again a type I functional response, therefore for further proof host exploitation pattern was examined by simple linear regression in above mentioned densities, and it was found that exploitation rate has been significantly increased (Type III functional response) in singleton and twin wasps ($P = 0.006$, $F = 7.96$ for singleton and $P = 0.03$, $F = 4.88$ for twin) whereas it remained unchanged in the other treatments ($P = 0.73$, $F = 0.119$ for triplet and $P = 0.48$, $F = 0.504$ for quadruplet, df = 1, 78 in all analysis), suggesting a density independence or a type I functional response.

Non-significant c and d parameters were excluded in all treatments which resulted in hyperbolic function of equation 1 to reduce to linear function of equation 2 with zero intercepts. A linear decrease in both parameters *a* of a type II functional response and *b* of a type III one was obvious with increasing intensity of superparasitism (Fig. 4).

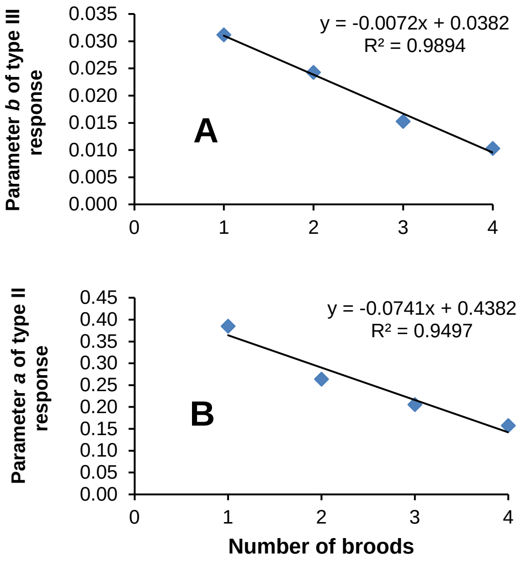

Figure 4 Changes in searching rate depending on number of broods/ host in *Ooencyrtus fecundus*, A.parameter (b) in type III functional response, and B. parameter (a) in type II functional response.

Discussion

Functional response curves resembled a type I functional response with constant mortality rates in densities below eight. Handling time is considered to be zero in a type I functional response model, whereas our direct observations showed that handling time was 11.40 - 14.28 min, implying that type I and type II functional responses are in fact the same and type I response can be obtained without exclusion of handling time. In this case, a type I response was produced because female egg load was higher than that required to parasitize all available hosts and wasps were not time-limited. Therefore, as long as the total time available exceeds that required to discover and handle all available hosts (as long as host density is less than daily fecundity), a type I functional response with complete host exploitation at lower densities is possible.

O. fecundus females appear to avoid superparasitism as long as unexploited hosts remain available, consistent with the observed departure of superparasitism frequencies from a Poison distribution. Other researchers also provide supporting data (Wu and Nordlund, 2002; Yamada and Ikawa, 2003; 2005). The negative effects of host-sharing for progeny fitness may explain this aversion to superparasitism (Ahmadpour *et al*., 2013). Given that *O. fecundus* can discriminate previously-parasitized hosts (Safavi, 1970; 1973), we may expect them to choose an adaptive superparasitism strategy. When unparasitized hosts are rare, females can gain offspring by superparasitizing, but not without incurring several costs. A singleton female will produce five percent more daughters than a twin female, and 42% more than a quadruplet female (Ahmadpour *et al*., 2013). However, the production of two daughters from a single host egg will result in 1.9 times more grand progeny than will production of a single daughter, and 2.8 times as many if four daughters are produced. Therefore, the relative scarcity of superparasitism would suggest that daughters arising from superparasitized hosts pay other, as yet unrecognized fitness costs, possibly in the form of dispersal ability, longevity, or survival. Even if taken into account that four broods of the same host waste half of the resources, still a 40% advantage is obtained. In contrast, some parasitoids such as *Metaphycus flavus* (Howard) (Hym., Encyrtidae) prefer parasitized *Coccus hesperidium* L. (Hem., Coccidae) to intact one (Tena *et al*., 2008). Some researchers state that parasitoids accept parasitized hosts when they have a high egg load or alternatively when they are approaching to the end of their reproductive life (Bouskila *et al*., 1995; Strand and Obrycki, 1996; Clark and Mangel, 2000).

Superparasitism was once considered maladaptive because it causes a parasitoid to waste both her eggs and searching time (Gardner *et al*., 1984). This is also true for *O. fecundus*. Reminding that each host egg has enough resources for the development of four parasitoid larvae, it can be expected that 4, 8 and 16 wasps may develop in densities 1, 2 and 4 host eggs respectively, if a full clutch is realized by the wasps. But the results revealed that 37.75 to 66% (average 50.66%) of this capacity was realized in different treatments. It indicates that competition between larvae resulted in wasting half of the resources.

Singleton and quadruplet wasps wasted respectively a minimum and maximum amount of resources, as > 55% and < 41% of potential host resources were exploited in three lower densities by the mentioned wasps. As a result, superparasitism could not fully compensate host deficiency (Table 3). For example, number of progeny at the density of 16 host eggs was 92-98% (average 95%) of that of the highest host density (32 sunn pest eggs); it means 14.7-17.5 wasps per 14.5-15.5 host eggs. It was 70-85% and 38-59% (average 49%) of the highest host density at densities of eight and four host eggs respectively. This occurred while wasps could theoretically realize 16 progenies (90% of their fecundity) at density of four host eggs. This is well supported by Godfray (1994) who stated that superparasitism may decrease natality in gregarious parasitoids due to scramble competition. These results indicate again negative effects of superparasitism on fertility; a result confirmed by other researchers (Carbone and Rivera, 2003 a, b: Tunça and Kilinçer, 2009). In the circumstances that chance of offspring is > 0 to survive, superparasitism may cause to gain fitness. Moreover, when intact or high quality hosts are rare, superparasitism can be adaptive (Bai and Mackauer, 1992). Rafat (2013) did not observe similar effects in *O. telenomicida* Vassilljev (the other congeneric species of sunn pest's egg parasitoid), perhaps due to his focus on singleton and twin progeny rather than more intensive levels of multiple attacks.

One may ask why similar reduction in progeny/host ratio did not occur in *per capita* number of progeny of triplets and quadruplets in lower densities. The lower competition level due to lower fecundity of the recent groups may be an explanation. However higher vulnerability of offspring during development also may be a reason of higher larval mortality even in intermediate densities, in which competition intensity has somewhat reduced. If this hypothesis were correct, it would suggest cumulative effects of superparasitism in sequential generations; a hypothesis that needs further proof by future studies. Convergence of number of progeny of different treatments at higher densities also may have the same interpretation. In other words, at lower host densities competition level is high and this affects smaller females and their progeny more than the larger ones, while at higher host densities competition intensity is low and larval mortality due to competition disappears, and female fecundity is the only source of variation between the wasps of different sizes. These results support the latter hypothesis (cumulative effects on larval mortality) rather than the former (reduced fecundity).

Searching efficiency of *O. fecundus* in this study was less than that of *Trissolcus semistriatus*, *T. grandis* and *T. vassilievi*, the other egg parasitoids of sunn pest in Asgari *et* *al*. (2001), Fathipour *et al*. (2000), Allahyari *et al*. (2004) and BenaMolaei *et al*. (2018a) investigations. Also maximum attack rate was considerably lower than reported in those studies. This may imply lower potential of *O. fecundus* in control of sunn pest. The mentioned parameters of *T. djadetshkoe* obtained by Abdi *et al*. (2015) was partially in the range of *O. fecundus* in this study.

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نشوونمای جمعی، بهره‌برداری از میزبان توسط *Ooencyrtus fecundus* (Hymenoptera: Encyrtidae) را تغییر می‌دهد

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چکیده: زنبور *Ooencyrtus fecundus* Ferriere & Voegele (Hymenoptera: Encyrtidae) پارازیتویید جمعی تخم سن گندم *Eurygaster integriceps* Puton می‌باشد. سوپرپارازیتیسم، ماده پارازیتویید را قادر می‌سازد که تولید چند فرزند به ازای یک میزبان نماید و بدین‌ترتیب زمان صرف شده برای جستجوی میزبان را کاهش دهد، ولی موجب تولید فرزندان کوچک و کوچک‌تر با افزایش تعداد افراد رقابت‌کننده برای منابع محدود میزبانی می‌شود. در این بررسی، این‌که آیا نشو و نمای جمعی موجب اثر روی واکنش تابعی زنبور *O. fecundus* در شرایط آزمایشگاهی (دمای ۲ ± ۲۶ درجه سلسیوس، رطوبت نسبی ۱۰ ± ۵۰ درصد و دوره نوری۱۶ ساعت روشنایی و ۸ ساعت تاریکی) می‌شود مورد آزمون قرار گرفت. تراکم‌های مختلف تخم میزبان (۱، ۲، ۴، ۸، ۱۶ و ۳۲) به ماده‌هایی عرضه شد که به‌صورت تکی، دوقلو، سه‌قلو و چهارقلو درون تخم‌های میزبان رشد یافته بودند. برای تعیین واکنش تابعی این ماده‌ها زمان کل ۵ ساعت براساس مشاهدات مستقیم زمان دستیابی و بیشینه نرخ حمله روزانه به‌ازای هر ماده درنظر گرفته شد. واکنش تابعی در زنبورهای تکی و دوقلو از نوع سوم و در زنبورهای سه‌قلو و چهارقلو از نوع دوم بود. با این وجود، در تراکم‌های تا ۸ تخم میزبان، تلفات ۱۰۰درصد بود که دلالت بر عدم وابستگی به تراکم میزبان در تراکم‌های پایین می‌نماید که مشخصه واکنش تابعی نوع اول می‌باشد. در واکنش تابعی نوع اول زمان دستیابی صفر منظور می‌شود، با این حال مشاهدات مستقیم نشان داد که زمان دستیابی در تیمارهای مختلف بین ۱۱/۴ تا ۱۴/۳ دقیقه متغیر بود. می‌توان نتیجه گرفت چنان‌چه وقت کافی برای یافتن و دستیابی تمام میزبان‌ها در تراکم پایین در دسترس باشد، واکنش تابعی نوع دوم به واکنش تابعی نوع اول انطباق پیدا می‌کند. با افزایش جثه پارازیتویید، کارایی کاوشگری افزایش و زمان دستیابی کاهش یافت.

واژگان کلیدی: بال غشائیان، Encyrtidae، *Eurygaster integriceps*، قدرت کاوشگری، واکنش تابعی