THE FORAGING BEHAVIOR OF *DIAERETIELLA RAPAE* (HYMENOPTERA: BRACONIDAE) ON *DIURAPHIS NOXIA* (HEMIPTERA: APHIDIDAE)

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Abstract - Host stage preference, functional response and mutual interference of *Diaeretiella rapae* (McIntosh) (Hymenoptera: Braconidae: Aphidiinae) on *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae) were investigated under defined laboratory conditions (20±1°C; 60±5% relative humidity; 16 h light/8 h dark photoperiod). Nicholson's model and linear regression were used to determine *per capita* search-efficiency and the interference coefficient, respectively. There was a significant difference between the rates of parasitism on different stages of *D. noxia*. The highest parasitism percentage was observed on the third instar nymphs of *D. noxia* in both choice and no-choice preference tests. Results of logistic regression revealed a type II functional response. The estimated values of search-efficiency (a) and handling time (T_h) were 0.072 h^{-1} and 0.723 h, respectively. The maximum attack rate was calculated to be 33.22. The *per capita* search-efficiency decreased from 0.011 to 0.004 (h^{-1}) as parasitoid densities increased from 1 to 8. Therefore, different host-parasitoid ratios can affect the efficacy of *D. rapae*.

Key words: Diaeretiella rapae, *Diuraphis noxia*, mutual interference, functional response

INTRODUCTION

The Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko) is regarded as an important cereal pest in many cereal-producing areas of the world, including Iran, (Liu et al., 2010) where it is widely distributed (Dolati, 2005). The aphid causes direct damage by sucking the sap of plants, and indirect damage by transmitting plant viruses, thereby causing tremendous yield losses in wheat at high infestation levels (Jones et al., 1989; Kindler and Hammon, 1996; Kruger and Hewitt, 1984; Von Wechmar, 1984). Feeding by *D. noxia* significantly decreased photosynthetic efficiency and substantially reduces grain yields (Smith et al. 1991, Burd and Elliott 1996).

A wide range of natural enemies have been recorded attacking this aphid (Aalbersberg et al., 1988; Noma et al., 2005; Tóth et al., 2009), among them the aphidiine parasitoids (Hym.: Braconidae, Aphidiinae) which have an important role in biocontrol of the aphids (Jones et al., 2003; Hopper et al., 1995; Starý, 1999). *Diaeretiella rapae* McIntosh is the main parasitoid of *D. noxia* (Noma et al., 2005; Rakhshani et al., 2008; Starý, 1999) and widely distributed in different parts of Iran (Rakhshani et al., 2008; Starý et al., 2000).

Host stage preference, functional response and mutual interference are among the most important behavioral characteristics to determine the efficiency of parasitoids for the biological control of aphids

(Luck, 1990). The functional response describes the relationship between the number of hosts parasitized per unit of time and density of hosts (McCaffrey and Horsburgh, 1986). Interference amongst adult parasitoids leads to a reduction in the parasitization rate as parasitoid density increases. One important mechanism that leads to inversely density-dependent patterns of parasitism is interference among parasitoids (Walde and Murdoch, 1988; Ives et al., 1999).

Many attempts have been made to investigate the foraging behavior of *D. rapae* (Ayal, 1987; Shukla et al., 1992; Pandey et al., 1984; Lu et al., 1992; Fathipour et al., 2006; Dashti et al., 2010; Abidi et al., 1987; Yu et al., 1993), of which few studies favor the interaction with *D. noxia* (Lester and Holtzer, 2002; Bernal et al., 1994). On the other hand, the numerical response of *D. rapae*, which corresponds to the mutual interference, has been the subject of a few researches on different aphids, (Pandey et al. 1986; Shulka et al., 1997). Since the host aphid has a critical impact on the behavioral characteristics of the parasitoids, here we paid special attention to the interaction of *D. noxia* and its most common parasitoid, *D. rapae,* in Iran (Rakhshani et al., 2008). In this study the response of *D. rapae* to various densities of *D. noxia*, as well as the effect of mutual interference among *D. rapae* females on parasitism rate and searching efficiency, were investigated.

MATERIALS AND METHODS

Insect culture

A population of RWA was originally collected from a wheat field in the suburb of Karaj - Tehran province, Iran, during October 2009. The aphid colony was reared on wheat (Pishtaz variety) in a growth chamber at temperature of 25±1°C, 60±5% relative humidity and a 16 h light/8 h dark photoperiod. The colony of *D. rapae* was initiated from adults, which were reared from mummies of *Brevicoryne brassicae* collected from a Canola field in the same region. Adult parasitoids were captured after emer-

gence and transferred to the culture of RWA in the above-mentioned rearing conditions, and allowed to propagate for several generations before use in the experiments. All experiments were performed as described above under colony rearing.

Host stage preference

Host stage preference was determined in two aspects of "*choice*" and "*no-choice*" preference experiments. By the *choice* preference assays, equal densities (ten individuals) of each nymphal instar (1st to 4th) and the newly emerged adults of *D. noxia* were exposed to a 1-day-old mated female parasitoid within the closed patch of a glass Petri dish (19 cm diameter). The parasitoids were removed after 12 h and the individuals of *D. noxia* were reared in separate cages until mummies appeared. The number of mummified aphids was recorded. The experiment was repeated ten times. In the *no-choice* preference experiment, fifty individuals of various *D. noxia* life stages were separately exposed to a 1-day-old mated female parasitoid in glass Petri dishes for 24 h. The experiments were performed for each nymphal instar and the adult stage, separately with ten replications. The data were analyzed using one-way ANOVA. If significant differences were detected, the means were compared by SNK; significant difference test (HSD; SAS Institute 2003).

Functional response

Densities of 2, 4, 8, 16, 32 and 64 third nymphal instars (preferred host stage) of RWA were prepared uniformly to create an arena for functional response experiments. Aphids of the different densities were placed on four wheat seedlings that had been planted in two 1.5 ml tubes, were transferred to BD Falcon™ 50 ml conical centrifuge tubes. Subsequently, a pair of male-female parasitoids was released into each container tube for a period of 24 h. Diluted honey (25%) was streaked across the micromesh-screened opening of the tube to feed the adult parasitoids during the experiment. The parasitoids were removed after 24 h

and the aphids were reared under normal rearing conditions until the formation of mummies. The numbers of healthy and mummified aphids were counted separately. The experiments were replicated ten times.

Mutual interference

A cohort of 450 third nymph instars of *D. noxia* were transferred onto wheat plants that had been planted in plastic pots (7.5 × 8 cm) covered with transparent isinglass (7.5 × 10 cm). A few holes covered with micromesh with diameters of 3 cm were prepared on the cover for ventilation. Different densities of female parasitoids (2 days old, mated) consisting 1, 2, 4, 6 and 8 were introduced inside the cages, separately. A streak that had been saturated with water and honey solution (25%) was placed inside the cage to feed the adult parasitoids. The parasitoids were allowed to oviposit for a period of 24 h and were then removed. The experiments were repeated ten times. The aphids were maintained on the wheat plants until the appearance of the mummies, which were counted and recorded separately for each density of aphid parasitoids.

Statistical Analysis

Data from functional response experiments were analyzed in two steps (Jouliano, 1993; De Clercq et al., 2000). In the first step, logistic regression was used to determine the type of functional response (Jouliano, 2001) as follows:

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

where N_a is the number of parasitized aphids, P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic and cubic parameters, respectively. The slope of the N_a near the lowest host density is a singularity of the functional response. Significant negative or positive linear coefficients (i.e., P_1) indicate the functional responses type II or III, respectively. The slope of the type II response declines (i.e., P_1 is negative), and the type III response accelerates (i.e., P_1 is positive).

In the second step, the search-efficiency (a) and handling time (T_h) were estimated using a type II equation for parasitoids without host replacement (Rogers, 1972) using the following equation:

$$N_a = N_0 \left[1 - \exp\left(-\frac{aT\,Pt}{aT_h N_0} \right) \right]$$

where N_a is the number of parasitized hosts, N_0 the initial density of hosts, T is the total time of the experiment, a the search-efficiency, P_t the number of parasitoids and T_h the handling time. The functional response models were analyzed using the SAS software (SAS Institute, 2003).

The *per capita* search-efficiency (a) of the parasitoid at the different parasitoid densities was evaluated by the following equation (Nicholson, 1933).

$$a = \left(1 / PT \right) \ln \left[N_t \Big/ (N_t - N_a) \right]$$

where N_t is the total number of hosts available (=450), N_a is the total of killed hosts, P is the number of parasitoids and T is the duration of the experiment (e.g. 24 h).

The interaction between the densities of parasitoids and search-efficiency were simulated using linear regression following the inductive model given by Hassell and Varley (1969).

$$a = Q\,P^{-m} \quad \text{or} \quad \log a = \log Q - m \log P$$

where a is the search-efficiency of the parasitoid, Q is the Quest constant, m is the mutual interference constant and P is the parasitoid density. In this model, m includes only the component of interference due to behavioral interactions between parasitoids, and not pseudo interference resulting from patch exploitation (Free *et al.* 1977).

All statistical comparisons were carried out with SPSS software ver. 16.1 using SNK tests with $P_{value} \leq 0.05$.

RESULTS

Host stage preference

Diaeretiella rapae oviposited in the various nymphal instars and adults of *D. noxia*. The mean percentage of parasitism by *D. rapae* on the various nymphal instars and adults are shown in Fig.1. There were significant differences between the number of parasitized hosts on the different stages of *D. noxia* both in the *choice* (F = 114.953; d.f. = 4, 45; $P_{value} \leq 0.05$) and *no-choice* (F = 191.905; d.f. = 4, 45; $P_{value} \leq 0.05$) preference tests. However, there was no significant difference in the percentages of parasitism in the third and fourth instar nymphs and adults of *D. noxia* (Fig. 1). On the other hand, the highest parasitism percentage was observed on the third instar nymphs of *D. noxia* in both *choice* and *no-choice* preference tests. Therefore the third instar nymph of *D. noxia* was used for the subsequent experiments.

Functional response

The functional response and rate of parasitism curves by *D. rapae* on different densities of RWA are shown in Fig. 2. The increases in host density lead to a decrease in the proportion of hosts parasitized by the parasitoid. The logistic regression analysis indicated a type II functional response (Table 1). The estimated values of searching efficiency (*a*) and handling time (T_h) were calculated as 0.072 h^{-1} and 0.723 h, respectively. The maximum attack rate (T/T_h) was determined to be 33.22 aphids/parasitoid/day.

Table 1. Results of logistic regression analysis of the proportion of *Diuraphis noxia* third instar nymphs parasitized by *Diaeretiella rapae* to initial host numbers.

Parameter	Estimate	SE
Intercept	1.4782	0.4439
Linear	-0.0507	0.0651
Quadratic	0.000435	0.00242
Cubic	-2.02E^{-6}	0.000024

Mutual interference

When the parasitoid density increased from 1 to 8, the *per capita* mortality rate decreased from 105.8 ± 2.97 to 29.269 ± 0.53 (Table 2). There were significant differences ($P_{value} \leq 0.05$) among the numbers of killed hosts per female parasitoid at the different densities of parasitoid (F= 298.85; d.f. = 4, 45; $P_{value} \leq$ 0.05). The *per capita* search-efficiency was estimated to be 0.011 ± 0.0001 h^{-1} when a single female parasitoid was observed in the aphid colony it decreased to 0.004 ± 0.000 h^{-1} at the density of 8 female parasitoids (Table 2). The relationship between search-efficiency and parasitoid density was described by this equation (R^2 = 0.973):

$$Log\ a = -1.92 - 0.505\ log\ P$$

Following the above equation, *m* (slope of regression line) was estimated as 0.505. The negative value of slope regression indicated that the search-efficiency decreases with an increase of parasitoid density. On the other hand, there was intra-specific competition among individuals of the female parasitoids in the high densities. The regression line of *D. rapae* on the third nymph instars of *D. noxia* is shown in Fig. 3.

DISCUSSION

We found that *D. rapae* prefer the third and fourth nymph instars of *D. noxia* in the course of two types of experiments. The same result was obtained by Bernal et al. (1994) and Lester and Holtzer (2002)

Table 2. *Per capita* parasitism and *per capita* search-efficiency (mean ± SE in both) of *Diaeretiella rapae* on *Diuraphis noxia*.

Parasitoid density	*Per capita* mortality rate	*Per capita* Searching efficiency
1	105.80± 2.97[a]	0.011 ± 0.000[a]
2	77.70±1.95[b]	0.009±0.000[b]
4	51.45±1.57[c]	0.006±0.0002[c]
6	37.87±1.02[d]	0.005±0.0002[d]
8	29.26±0.53[e]	0.004±0.0001[e]

who tried to find the most suitable host stage for functional response experiments. In another study with a different aphid, *Brachycorynella asparagi* (Mordwilko) (Hemi: Aphididae), Hayakawa et al. (1990) found that the third and fourth instar nymphs of *D. noxia* were the most preferred stages for *D. rapae*. Different patterns of host stage preference for *D. rapae* have been reported for 2nd instar nymphs of *Schizaphis graminium* (Rondani) (Dashti et al., 2010) and *Brevicoryne brassicae* (L.) (Fathipour et al., 2006). It seems that the preference of last nymphal instars is a more common occurrence in some other aphidiine species, such as *Aphidius matricariae* (Holiday) - *Aphis gossypii* Glover (Talebi et al., 2006) and *Aphis fabae* Scopoli (Tahriri et al., 2007). Similarly, the walnut aphid parasitoid, *Trioxys pallidus* (Haliday) preferred the third and fourth instar nymphs of the walnut aphid, *Chromaphis juglandicola* (Kaltenbach) (Rakhshani *et al.* 2004). It is worthwhile noting that when the

aphid parasitized in the third and fourth instars, they emerge as adults and reproduce before being killed (Starý 1988), as phenomena observed for *D. rapae*. On the other hand, it can be an adaptive strategy to reduce the risk of pre-imaginal mortality in younger instars (Lin and Ives, 2003)

The functional response of *D. rapae* on *D. noxia* was identified as type II, which has also been reported for *D. rapae* on different densities of *Myzus persicae* (Sulzer), *Brevicoryne brassicae* (L.) and *D. noxia* (Mordvilko) as well (Lu et al., 1992, Shukla et al., 1992, Yu et al., 1993, Bernal et al., 1994, Lester and Holtzer 2002, Fathipour et al., 2006). Type II functional response has frequently been reported in other aphid parasitoids, including *Aphidius ervi* Haliday on *Acyrthosiphon pisum* (Harris) (Ives *et al.* 1999), *Aphidius sonchi* Marshall on *Hyperomyzus lactucae* (L.) (Liu 1985), *Aphidius nigripes* Ashmead on *Macrosiphum euphorbiae* (Thomas) (Cloutier
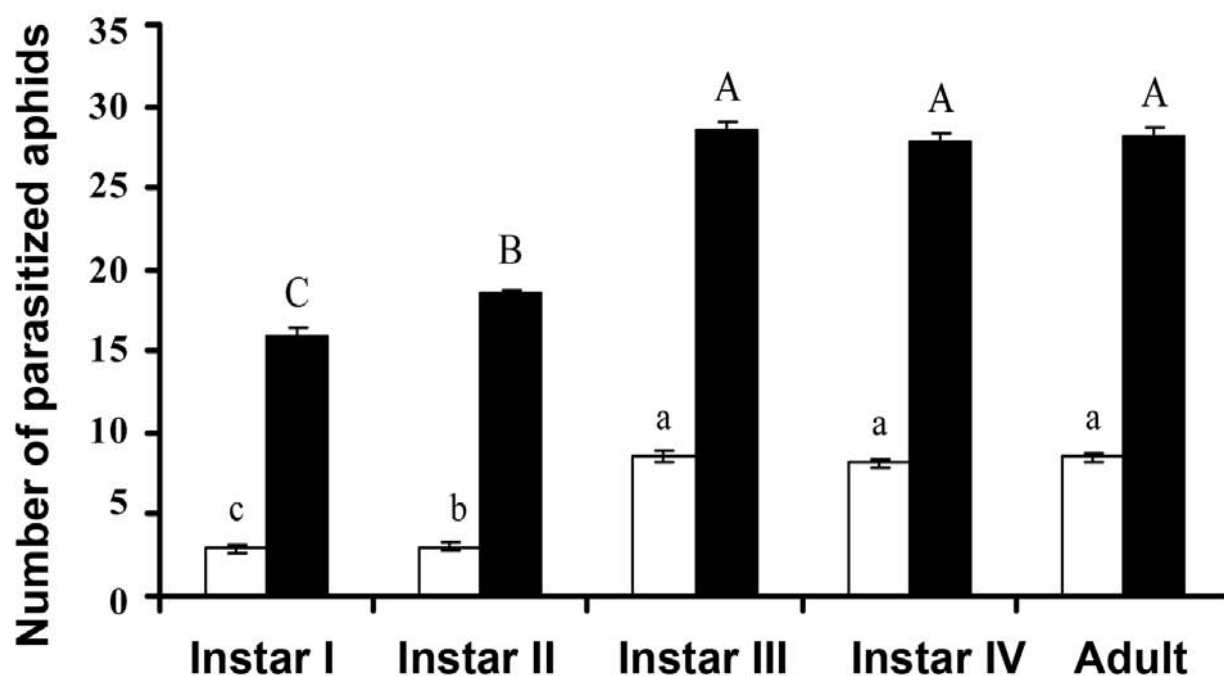

Fig. 1. Host stage preference of different life stages of *Diuraphis noxia* parasitized by *Diaeretiella rapae* in *choice* (lower case letters) and *no-choice* (upper case letters) tests. Values followed by different letters are significantly different ($P < 0.05$). (□) Choice; (▪) no choice.
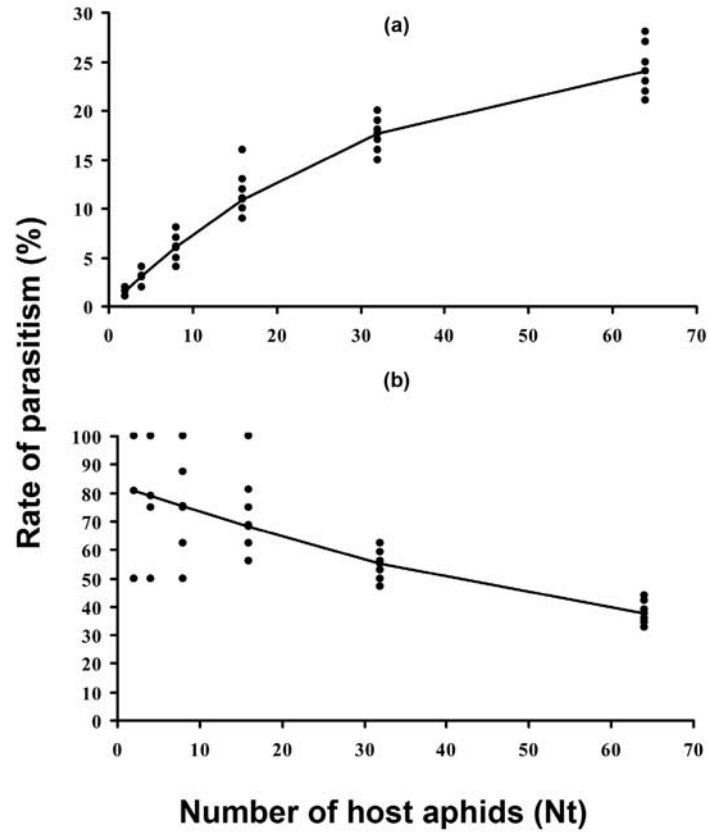
Fig. 2. Type II functional response of *D. rapae* (a) and percentage parasitism (b) on different densities of third nymph instars of *D. noxia*.
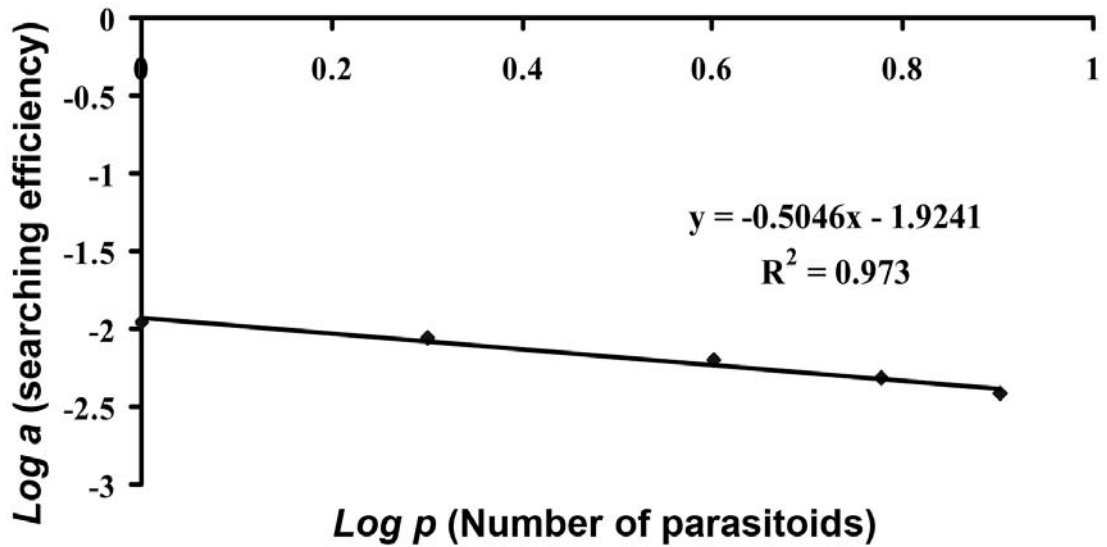

Fig. 3. The regression line in mutual interference of *D. rapae* on *D. noxia*.

and Holling 1984), *Aphidius smithi* Sharma and Subba Rao on *Acyrthosiphon pisum* (Harris) (Mackauer 1983), *L. fabarum* on *Aphis craccivora* Koch (Takalloozadeh et al., 2004), *A. matricariae* and *A. colemani* on different densities of *A. gossypii* (Zamani et al., 2006) and *Aphidius matricariae* (Holiday) on *Aphis fabae* (Scopoli) (Tahriri et al., 2007). Type III functional response has previously been reported for *D. rapae* on *Lipaphis erysimi* (Kalt) (Pandey et al., 1984) and *Schizaphis graminium* (Rondani) (Dashti et al., 2010), *A. colemani* and *Lysiphlebus testaceipes* Cresson on *Schizaphis graminium* (Rondani) (Jones et al., 2003), *T. indicus* on *A. craccivora* (Singh and Sinha 1983) and *T. pallidus* on *C. juglandicola* (Rakhshani et al., 2004). When the parasitoids are limited for a fixed time to search for hosts, generally a decelerating (type II) functional response curve is displayed (Burnett, 1951; Griffiths, 1969; Allen and Gonzalez, 1975; van Lenteren and Bakker, 1978; Collins et al., 1981; Hertlein and Thorarinsson, 1987). Several factors such as host species, host densities, previous experiences and temperature may affect the type of functional response (Juliano and Williams, 1985; Coll and Ridgway, 1995; Runjie et al., 1996; Messina and Hanks, 1998; Wang and Ferro, 1998; De Clercq et al., 2000; Mohaghegh et al., 2001; Moezipour et al., 2008). It may also depend on the different geographical race of the parasitoid species (van den Bosch et al., 1979), an important aspect of the Iranian population of *D. rapae*. Both type II and III responses in parasitoids relate to some degree of success, including establishment and partial control. It must also be noted that not all functional response studies considered are comparable in terms of analysis and experimental set-up. Indeed, the results of functional response experiments may be overestimating type II curves. For instance, it has been suggested that time-limited experiments may force a type II curve on the insects' behavior (van Lenteren and Bakker, 1976; Walde and Murdoch, 1988; Ives et al., 1999).

The searching efficiency (*a*) and handling time (T_h) of *D. rapae* to different densities of *D. noxia* were reported to be 1.341 h⁻¹ and 0.408 h, respectively at 21°C, relative humidity of 50-70 % and a 14 h light/10

h dark photoperiod (Bernal et al., 1994) and 1.74 h⁻¹ and 0.024 h, respectively (Lester and Holtzer, 2002), both of them showing greater values from those we estimated. This may arise from variations in the populations of hosts and parasitoids, or different conditions of experiments in the laboratory.

The maximum rate of parasitism for *D. rapae* on different densities of third nymphal instar of *D. noxia* for the random parasitoid equations was estimated to be 33.22 per day, higher than the estimated value of 23.53 (at 25°C) reported by Fathipour et al. (2006) when the host aphid was *B. brassicae*. Conversely, our results indicated that the estimated values of handling time for the random parasitoid equations were 0.723 h (0.03 day) lower than value of 1.02 day (at 25°C) reported by Fathipour et al. (2006) for *D. rapae* on *B. brassicae*. This clearly means that *D. rapae* is a more effective parasitoid for the control of *D. noxia* compared to *B. brassicae*.

There were negative relationships between search-efficiency and parasitoid density in the experiments of mutual interference. The number of killed hosts per parasitoid decreased with an increase in the number of female parasitoids, too. Intra-species competition for the female parasitoids leads to more time being spent for host finding (Shukla et al., 1997; Pandey et al., 1986; Abidi et al., 1989; Fathipour et al., 2006). The searching efficiency of parasitoids at densities of 1 and 8 parasitoids was estimated to be 1.173 and 0.205 per 1 day, respectively (Fathipour et al., 2006). In our study, the obtained *a* value was lower than in the above study.

In general, differences in the density of host aphids and the respective parasitoids influence the behavioral characteristics. A higher density of parasitoid may increase the proportion of male progeny, because males need less food resources than females (Jones et al., 1999).

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