Functional response and mutual interference of *Diaeretiella rapae* (Hymenoptera: Aphidiidae) on *Brevicoryne brassicae* (Homoptera: Aphididae)

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Functional response and mutual interference are the most important behavioural characteristics that reveal different aspects of host–parasitoid interactions. In this study, functional response and mutual interference of the parasitoid wasp, *Diaeretiella rapae* (M'Intosh) attacking the cabbage aphid, *Brevicoryne brassicae* (Linnaeus) were investigated. Logistic regression was used to distinguish the shape of the functional response (type II or III). Nonlinear least-square regression was used to estimate the attack rate (a) and handling time (T_h). Nicholson's model and linear regression were used to determine per capita searching efficiency and interference coefficient, respectively. Logistic regression suggested a type II response on *B. brassicae* nymphs. The per capita parasitism decreased significantly from 80.80 (67.33%) to 11.85 (9.88%) as parasitoid densities increased from 1 to 8 females. Consequently, the per capita searching efficiency decreased significantly from 1.173 to 0.205 as parasitoid densities increased from 1 to 8. The rate of parasitism increased as the host density increased from 2 to 50, and subsequently the parasitoid density decreased from 8 to 1. Therefore, different host–parasitoid ratios could affect the efficacy of *D. rapae*.

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1. Introduction

The cabbage aphid, *Brevicoryne brassicae* (L.) is a pest of cruciferous plants, especially cabbage, occurring in various parts of the world. The aphid causes direct and indirect damage by sucking the sap of plants and transmitting plant viruses (Ellis *et al.* 1998, Blackman & Eastop 2000, Schliephake *et al.* 2000). *B. brassicae* prefers feeding on younger plant tissues, which makes it an important aphid on *Brassica* as it renders the head as unmarketable. Control of the aphid is commonly achieved by repeated application of insecticides. The development of resistance to insecticides and adverse effects on natural enemies highlights the need for less insecticide-dependent methods of pest control (Verkerk *et al.* 1998). One of the control measures, which can be used for the cabbage aphid, is biological control. The aphid is attacked by the parasitoid *Diaeretiella rapae* (M'Intosh), which tends to specialize on crucifer-feeding aphids. However, attack on a range of plant families by numerous other species of aphids has been reported too (Dhiman & Kumar 1987, Costello & Altieri 1995, Bernal *et al.* 2001, Lester & Holtzer 2002).

Before using a parasitoid in a biological control programme, it is essential to know about the efficiency of the parasitoid. One of the important methods to assess the efficacy of natural enemies is the study of behavioural characteristics, including foraging behaviour. Study of parasitoid behaviour is an important key to understanding how the insects live, how they influence the population dynamics of their hosts, and how they influence the structure of the insect communities in which they exist (Jervis & Kidd 1996). It is thus a necessary prerequisite for the selection of natural enemies for biological control programmes and for the evaluation of their performance after their release (Luck 1990).

Two important behaviours of parasitoids are functional response and mutual interference. Functional response is the number of hosts successfully attacked per predator (parasitoid) as a function of prey (host) density (Solomon 1949). It describes the way a natural enemy responds to the changing density of its prey (host) by killing (parasitizing) more or fewer individuals, and it is a commonly measured attribute of natural enemies of pests (Bazzocchi & Burgio 2001). Holling (1959) considered three types of functional response. In the type I, there is a linear relation between prey density and the number of preys killed, while in the type II it is curvilinear and saturation level is reached in a gradual way. The type III is described by a sigmoid relation and considered to be a regulating factor in the population dynamics of the pest and the natural enemy. The functional response of a parasitoid is a crucial factor in the population dynamics of host–parasitoid systems. This behaviour can determine if a parasitoid is able to regulate the density of its hosts (Schenk & Bacher 2002). Functional response models help to evaluate two vital parameters, handling time (i.e. the time that it takes a parasitoid to encounter and parasitize a single host), and attack rate (i.e. the rate at which a parasitoid searches). Several studies (Pandey *et al.* 1984, Abidi *et al.* 1987, Lu *et al.* 1992, Shukla *et al.* 1992, Yu *et al.* 1993, Bernal *et al.* 1994, Lester & Holtzer 2002) have been carried out on the functional response of *D. rapae* to different densities of other aphids such as *Myzus persicae* (Sulzer), *Diuraphis noxia* (Mordvilko) and *Lipaphis erysimi* (Kalt.). Less attention, however, has been paid to cabbage aphid, *B. brassicae*. In most available literature, the functional response of *D. rapae* to different densities of aphids has been determined as the type II. In the studies reported by Pandey *et al.* (1984) and Abidi *et al.* (1987), *D. rapae* displayed functional response of type III to mustard aphid (*Lipaphis erysimi*). The type of functional response and the rates of its parameters (attack rate and handling time) are influenced by different factors such as natural enemy and host species, physical conditions in the laboratory, and the variety of the host plant, etc. (Coll & Ridgway 1995, Messina & Hanks 1998, Fathipour *et al.* 2001).

Aggregation by parasitoids to host patches is an integral component of models of host–parasitoid population dynamics. In discrete-time models, aggregation in space to host patches stabilizes the host–parasitoid interaction by causing searching efficiency to decrease with increasing parasitoid density (Godfray & Pacala 1992, Cronin & Strong 1993a). Inverse density dependence in searching efficiency is known as parasitoid interference or mutual interference (Beddington 1975). The study of mutual interference was initiated by Hassell and Varley (1969), who noted an inverse relation between the parasitoid searching efficiency and the density of searching parasitoids. Such a relation is to be expected, because as parasitoid density increases, individual parasitoids will waste an increasing proportion of their searching time to encounter other conspecifics. According to the literature, the parasitoid interference has been reported to occur commonly in the laboratory, but it has been hardly ever reported by field studies. Significant interference has been reported among populations of parasitoids both in many laboratory experiments and some field experiments (Cronin & Strong 1993 a,b). Significant mutual interference was reported among *D. rapae* females parasitizing *Lipaphis erysim* (Pandey *et al.* 1986, Abidi *et al.* 1989, Shukla *et al.* 1997).

In this study, the functional responses of

D. rapae to various densities of second instar nymphs of *B. brassica* were investigated and the handling time and the attack rate of the parasitoid were estimated. We examined the effects of mutual interference among *D. rapae* females on per capita parasitism and searching efficiency.

2. Materials and methods

2.1. Parasitoid and host cultures

Diaeretiella rapae used in this study was originally collected from mummified aphids (*Brevicoryne brassicae*) in an infested cabbage field at the College of Agriculture of Tarbiat Modarres University (Tehran) in May 2002. The first laboratory generation of wasps was used to conduct the experiments. The *B. brassicae* culture was originally started from individuals collected from the above cabbage field and kept in a growth chamber on cabbage plants. Both parasitoid and aphid individuals were kept in a growth chamber at 25±1ºC, 60±5% r.h. and a photoperiod of L16:D8 h.

2.2. Functional response

The experimental arena consisted of a Plexiglas cage (4×8×14 cm) with a micromesh screen on the lid for ventilation. Distilled water and honey solution (10%) were placed in cages as the parasitoid food. Second instar nymphs of *B. brassicae* were randomly placed on the cabbage leaves inside the cages at densities of 2, 4, 6, 8, 10, 15, 20, 30, 40 and 50 per cage. A single female parasitoid (maximum 24 hours old) was introduced into each cage. Each host density was replicated 10 times. After 24 hours, the parasitoids were removed and the hosts were maintained in a growth chamber until all parasitized (mummified) aphids were recognized. The experiment was conducted at 25±1ºC, 60±5% r.h. and a photoperiod of L16:D8 h.

Two principal steps underlie the statistical analysis of the functional response: 1) model selection, and 2) hypothesis testing (Juliano 1993, De Clercq *et al.* 2000). In the first step, a logistic regression analysis was made of the proportion of hosts parasitized as a function of initial density. The proportion of hosts parasitized declines monotonically with prey density in the type II response, but is positively density-dependent over some region of host density in the type III response (De Clercq *et al.* 2000). The sign of the linear coefficient estimated by the logistic regression (negative or positive) can be used to distinguish the shape of the functional response curve (type II or type III, respectively) (Juliano 1993, Messina & Hanks 1998, De Clercq *et al.* 2000). In the second step, both the disc equation (Holling 1959) (Eq. [1]) and the random parasitoid equation (Royama 1971, Rogers 1972) (Eq. [2]) were used to obtain estimates for handling time (T_h) and searching efficiency or attack rate (a). For the type II response, the equations are as follows:

$$N_a = (a\,T\,N_t) / (1 + a\,T_h\,N_t) \tag{1}$$

$$N_a = N_t\,[1 - exp\,(a\,(T_h\,N_t - T))] \tag{2}$$

where N_a is the number of parasitized hosts, N_t, the number of hosts offered, T, the total time available for the parasitoid, a, the attack rate (searching efficiency), and T_h the handling time.

Statistical analyses were performed using the SAS package (SAS Institute 1989). In order to estimate the handling time and searching efficiency, nonlinear regression, using the least square method with DUD initialization, was used. Further, the predicted number of parasitized hosts for a given host density was also determined.

2.3. Mutual interference

The experimental arena and growth chamber conditions were the same as those used in the functional response experiment. Host density was held constant at 120 second instar nymphs of *B. brassicae*. Female parasitoids at densities of 1, 2, 4, 6 and 8 per cage were allowed to search the hosts for 24 h. Each combination of hosts and parasitoid density was replicated 15 times. In the end of each experiment, the parasitoids were removed and the cabbage leaf with aphid nymphs was placed in growth chamber for development of the parasitoids.

The per capita searching efficiency (a) of the parasitoids at different parasitoid densities was calculated by the following equation (Nicholson 1933):

$$a = (1 / P\,T)\; ln\; [N_t / (N_t - N_a)] \tag{3}$$

where N_t is the total number of hosts available (=120), N_a is the total number of hosts attacked, P is the number of parasitoids, and T is the duration of the experiment (set to 1.0 for one day).

Searching efficiency was plotted against parasitoid density, both on a logarithmic scale. The points were fitted to a linear regression by the least square method, using the following inductive model given by Hassell and Varley (1969), assuming the parameter m as a slope and Q as the intercept of the regression line:

$$a = Q\,P^{-m} \text{ or } log\; a = log\; Q - m\; log\; P \tag{4}$$

where a is the searching efficiency of the parasitoid, Q is the quest constant, and m is the mutual interference constant. In this model, m includes only the component of interference due to behavioural interactions between parasitoids, not pseudointerference resulting from patch exploitation (Free *et al.* 1977).

3. Results

3.1. Functional response

Functional response and percentage parasitism curves are depicted in Fig. 1. The logistic regression analysis (Table 1) indicated a type II functional response. The estimate of the linear coefficient was significantly different from 0 (p<0.01) and its value was –0.159.

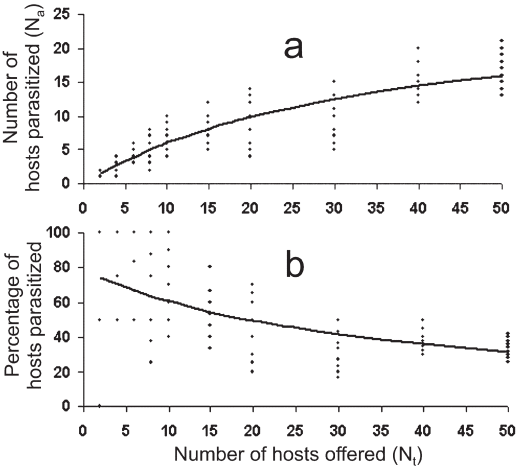

Fig. 1. Functional response (a) and percentage parasitism (b) of *D. rapae* on *B. brassicae* second instars. Symbols and lines represent the observed and predicted numbers (Holling disc equation), respectively.

Attack rate and handling time for the disc equation were 0.033±0.03 h^{-1} and 0.892±0.102 h, respectively, and for the random parasitoid equation they were 0.049±0.007 h^{-1} and 1.020±0.115 h, respectively (Table 2).

The lower coefficient of determination [r^2 = 1–(residual sum of squares / corrected total sum of squares)] for the disc equation and the random parasitoid equation were thus 0.77 and 0.76, respectively. The estimated maximum rate of parasitism (T/T_h) for the disc equation and the random parasitoid equation were determined as 26.91 and 23.53, respectively.

The rates of r^2 and standard errors of the estimated parameters indicated that both equations (disc equation and random parasitoid equation) adequately describe the functional response of *D. rapae*.

Table 1. Results of logistic regression analysis of the proportion of *B. brassicae* second instars parasitized by *D. rapae* females to initial host numbers.

Parameters	Estimate	*S.E.*	χ^2	*p*
Constant	1.9825	0.3499	32.10	<0.0001
Linear	–0.1595	0.0487	10.73	0.0011
Quadratic	0.00304	0.00189	2.58	0.1085
Cubic	–0.00002	0.000022	0.66	0.4149

Table 2. Parameters (mean ± *S.E.*) estimated by disc and random parasitoid equations, evaluating functional response of *D. rapae* females to densities of *B. brassicae* nymphs.

	Disc equation			Random parasitoid equation		
Type	a(h^{-1})	T_h(h)	r^2	a(h^{-1})	T_h(h)	r^2
II	0.033±0.003	0.892±0.102	0.77	0.049±0.007	1.020±0.115	0.76

Table 3. Per capita parasitism and per capita searching efficiency (mean ± *S.E.* in both) of *D. rapae* on *B. brassicae*.

Parasitoid densities	Per capita parasitism	Per capita searching efficiency
1	80.800±4.210 ^{a}	1.173±0.112 ^{a}
2	48.150±1.370 ^{b}	0.839±0.056 ^{b}
4	22.750±0.948 ^{c}	0.373±0.031 ^{c}
6	14.983±0.671 ^{d}	0.244±0.022 ^{d}
8	11.853±0.402 ^{e}	0.205±0.016 ^{d}

Values followed by different letters within columns are significantly different ($p<0.01$).

3.2. Mutual interference

The per capita parasitism (aphid nymphal mortality) decreased significantly from 80.80 (67.33%) to 11.85 (9.88%) with increasing parasitoid densities from 1 to 8 per 120 host nymphs ($F_{4, 45}=198.51$, $p<0.001$; Table 3). Consequently, the per capita searching efficiency also decreased significantly from 1.173 to 0.205 with increasing parasitoid densities from 1 to 8 ($F_{4, 45}=51.63$, $p<0.001$; Table 3).

The linear regression between the logarithm of per capita searching efficiency and the logarithm of parasitoid density in the mutual interference analysis resulted in the equation:

$$\log a = 0.115–0.895 \log P \ (F_{1,3}= 140.29, \ p<0.001, \ r^2= 0.97).$$

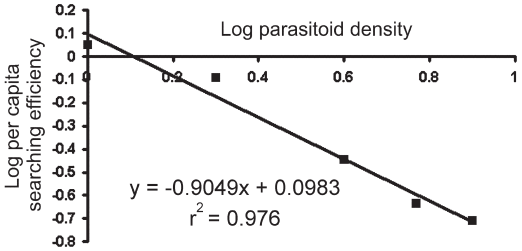

Fig. 2. Regression line in mutual interference of *D. rapae*.

The interference coefficient (slope of the regression line) is m=–0.895. The negative value of the regression slope indicates an inverse relationship between parasitoid density and per capita searching efficiency. In other words, searching efficiency decreases with increasing parasitoid density. The regression line is illustrated in Fig. 2 using logarithmic axes.

4. Discussion

D. rapae is the most abundant and important natural enemy of *B. brassicae* in Iran and plays a major role in reducing the population density of its host. In addition to *D. rapae*, there are some other parasitoid wasps in Iran, which are less abundant and less important such as *Aphidius* spp. and *Lysiphlebus* spp. from the same family (Aphidiidae) that parasitize cabbage aphid (Stary *et al.* 2000). Among the natural enemies of cabbage aphid, *D. rapae* serves as a good candidate for natural support, mass rearing and release for controlling this aphid because of high population densities and high rates of parasitism. In this regard, the study of foraging behaviour and demographic parameters of *D. rapae* in a host-parasitoid system is essential. Some demographic parameters of *D. rapae* and *B. brassicae* were calculated and compared by Hosseini *et al.* (2003). They inferred that population growth rate of the parasitoid was slightly less than that of the aphid.

In this study, different densities of host and parasitoid were selected according to the literature. The main purpose of the selection of these densities was to identify the role of different densities of the host and parasitoid on the foraging behaviour of the parasitoid and on the host-parasitoid interactions. The selected densities may not be completely compatible with those of the host and parasitoid in natural populations.

4.1. Functional response

The type II functional response displayed by *D. rapae* to different densities of *B. brassicae* nymphs is characteristic of many aphid parasitoids, though the type III responses have also been reported (Bernal et al. 1994). In most related literature, the functional response of *D. rapae* to different densities of *Diuraphis noxia* (Bernal *et al.* 1994, Lester & Holtzer 2002), *Lipaphis erysimi* (Shukla *et al.* 1992, Yu *et al.* 1993) and *Myzus persicae* (Lu *et al.* 1992) has been determined to be of the type II. However, in the studies reported by Pandey *et al.* (1984) and Abidi *et al.* (1987), *D. rapae* displayed a type III functional response to mustard aphid (*Lipaphis erysimi*).

The estimated maximum attack rate has been determined as 28.8 per 0.5 h (Abidi *et al.* 1987), 41.84 (at 15°C) and 47.56 (at 18°C) per 24 h (Yu *et al.* 1993) and 59.5 per 24 h (Bernal *et al.* 1994). In this study, the estimated maximum number of parasitized aphids is much smaller than that obtained by the above researchers.

The rates of searching efficiency (a) and handling time (T_h) were reported to be 1.341 h^{-1} and 0.408 h, respectively (Bernal *et al.* 1994) and 1.74 h^{-1} and 0.024 h, respectively (Lester & Holtzer 2002). The cited rates of *a* are greater and T_h are smaller than those obtained in our study. However, the differences among the experimental conditions such as host species and physical conditions between different studies were substantial.

For the type II response, parasitism is not density dependent: that is, the intensity of parasitism does not increase with host density (Hassell 1978). Several authors (sources) have tried to explain why the type III response is less common than the type II. They agree that in laboratory tests, parasitoids are forced to remain in the patch, whereas under natural field conditions they would probably leave the patch because of the very low host density or because most hosts are already parasitized (Montoya *et al.* 2000).

Bernal *et al.* (1994) pointed out that the relation between functional responses observed in the laboratory and field performance of natural enemies is not clear, but some studies showed a significant difference between the responses observed in laboratory and field environments. It is recognized that functional response derived from laboratory studies may bear little resemblance to those that could be measured in the field (Montoya *et al.* 2000).

Houck and Strauss (1985) pointed out, however, that studies of functional response in laboratory could be used to infer basic mechanisms underlying natural enemy-host interactions. Such studies provide valuable information for biological control programmes. Bernal *et al.* (1994) expressed that during biological control evaluation processes, comparisons of parameter values of two or more parasitoids may be more meaningful and convenient than similar comparisons involving functional response curves.

4.2. Mutual interference

In the present study, the percentage of parasitized aphids increased with increasing parasitoid density; however, the increased parasitoid density resulted in a constant decrease in the number of aphids killed per parasitoid, as well as reduced progeny per parasitoid. The searching efficiency of the parasitoid decreased with increasing parasitoid density, and the stability of co-existence between the host and the parasitoid increased with an increase in mutual interference (Jones *et al.* 1999).

Shukla *et al.* (1997) reported that when 1, 2, 4 or 8 parasitoids (*D. rapae*) were released on 200 aphids (*Lipaphis erysimi*), the number of emerged parasitoids showed a significant positive correlation with increasing parasitoid density. However, the rate of multiplication, expressed as parasitoid egressed/female parasitoids put in, was the highest with one parasitoid per 200 hosts and decreased with an increasing parasitoid number. The fact that more parasitoids have a lower rate of multiplication shows the existence of mutual interference. The number of progeny produced per female *D. rapae* parasitoid is inversely proportional to the parasitoid number, indicating intraspecific competition in the parasitoid (Abidi *et al.* 1989). Pandey *et al.* (1986) studied the numerical response of *D. rapae* with *Lipaphis erysimi*. They concluded that the number of offspring emerging was positively correlated with parasitoid density. However, the rate of multiplication was greatest with one parasitoid per 100 hosts and decreased non-linearly with an increase in parasitoid density. It was suggested that mutual interference occurred between parasitoids. The results of our study on the effect of *D. rapae* density on its per capita parasitism and searching efficiency are consistent with the results reported by Abidi *et al.* (1989) and Pandey *et al.* (1986).

Mutual interference of parasitoids in parasitizing their host refers to intraspecific competition. The effect of this competition is a measurable density-dependent process. High parasitoid density or low parasitoid-host ratios may result in longer development time and smaller size of parasitoid progeny, due to possible differences in nutritional quantity as a consequence of host-feeding or superparasitism, which will result in exhaustion of food for developing parasitoids. As parasitoid-host ratios increase, it is possible that parasitoids are able to select more suitable hosts, the result being that, on average, the progenies are larger, live longer and develop more rapidly. High parasitoid density yields a high proportion of male progeny, probably because females tend to oviposit unfertilized eggs. In addition, males could attain maturity on less food than females in some species (Jones *et al.* 1999). The mutual interference is important and practical in mass rearings and release projects of parasitoids.

The results of this study serve to increase our knowledge on one of the most important parasitoids of *B. brassicae*. They also serve to provide information for comparing the relative efficiencies of other candidate species of parasitoids for possible mass propagation for augmentation against *B. brassicae*.

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