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Temperature-Dependent Functional Response of *Diaeretiella rapae* (Hymenoptera: Braconidae), a Parasitoid of *Diuraphis noxia* (Hemiptera: Aphididae)

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ABSTRACT

The effects of host density and temperature on the functional response of *Diaeretiella rapae* (M'Intosh) parasitizing *Diuraphis noxia* (Mordvilko) were evaluated at six constant temperatures (10, 15, 20, 25, 30 and 32.5°C) and six host densities (2, 4, 8, 16, 32, and 64 numbers). A type II functional response was obtained at all temperatures tested. The maximum parasitism rate was observed in density of 64 hosts, ranged from 3.00±0.67 at 10°C to 24.20±0.94 at 25°C. The searching efficiency (*a*) was highest at 15°C and then decreased linearly as the temperature increased to 32.5°C. The searching efficiency ranged from 0.080±0.008 h^{-1} at 15°C to 0.032±0.017 h at 10°C. The estimated value of handling time (T_h) decreased linearly with increasing temperature from 10 to 25°C. The maximum rate of parasitization was observed at 15, 20 and 25°C (32.94, 32.22 and 36.51 nymphs/24 h, respectively). The results suggest that *D. rapae* has potential as a biocontrol agent of *D. noxia* and warrants further evaluation in the field conditions.

Key words: Russian wheat aphid, biological control, parasitoid wasp.

INTRODUCTION

The Russian wheat aphid (=RWA), *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), is an important pest of Poaceae concentrating particularly on wheat and barley in Iran (Rezvani, 2001). This aphid has expanded its range into new cereal producing areas of the world and is now a major economic pest on barley and wheat in many cereal-growing areas of the world (Hughes and Maywald, 1990; Pike and Allison, 1991).

The braconid wasp, *Diaeretiella rapae* (M'Intosh), is a solitary endoparasitoid of a wide range of aphids including *Brevicoryne brassicae* (L.) (Fathipour *et al*., 2006), *D. noxia* (Bernal *et al*., 1994; Lester and Holtzer, 2002; Farid *et al*., 1998) and *Lipaphis erysimi* Kaltenbach (Abidi *et al*., 1987).

An important goal of basic ecological studies is to determine which attributes of parasitoids contributed to the success of biological control (Beddington *et al*., 1978). The behavioural response of parasitoids to host density is potentially related to its success (Huffaker *et al*., 1971; Berryman, 1999). This is described by the functional response, the relationship between prey or host density and the attack rate of predators or parasitoids (Solomon 1949; Holling, 1959).

Several studies have been conducted on the functional response of *D. rapae* on different aphid species such as *B. brassicae* , *D. noxia*, *M. persicae, L. erysimi* and *Schizaphis graminum* (Rondani) (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 and Holtzer. 2002; Fathipour *et al*., 2006; Dashti *et al*., 2010), but no detailed study has been conducted on the functional response of *D. rapae* at various constant temperatures. There is some evidence indicating that temperature can influence the functional response of parasitoids (Mack *et al*., 1981; Flinn, 1991; Gitonga *et al*., 2002; Zamani *et al*., 2006). Therefore, the objective of the current study was to determine the effect of temperature on the functional response of *D. rapae* to varying densities of *D. noxia*. Using the results from these studies, we discuss about optimum temperatures to use *D. rapae* in a biological control program against *D. noxia*.

MATERIAL AND METHODS

Aphid and Parasitoid Cultures

A population of RWA was originally collected from a wheat field in suburbs of Karaj, Iran in October 2009. The aphids were reared on wheat (Pishtaz variety) in a growth chamber at 25±1°C, 60±5% relative humidity and a photoperiod 16: 8 h (Light: Dark) for several generations. A colony of *D. rapae* was established from mummies of *B. brassicae* from infested canola field at the college of Agriculture, Tarbiat Modares University (Tehran) in April 2010. Newly emerged adults of *D. rapae* were transferred and reared on Russian wheat aphid at 20±1°C, 60±5% relative humidity and a photoperiod 16: 8 h (Light: Dark) for one generation.

Functional response

In order to determine the functional response of *D. rapae* to various host densities, individual parasitoid wasps were exposed to six host densities (treatments) (2, 4, 8, 16, 32, and 64 hosts per arena) at six constant temperatures (10, 15, 20, 25, 30 and 32.5°C). The experimental arena consisted of cylindrical plastic vials (3 cm diameters and 11.5 cm height) that contained two wheat seedlings (3 leaf stage). Two drops of 20 % honey water solution were dropped onto the inner wall of the cylindrical plastic vial as food for feeding of adult parasitoids. Before initiating the functional response experiments we determined that *D. rapae* preferred third-instar nymphs of RWA (Tazerouni *et al*., 2011), therefore we used this life stage in functional response experiments. For each host density, a pair of male and female of newly emerged parasitoids (<24 h old) was introduced into each arena for 24 h and then removed.

The arenas with exposed nymphs were placed in an incubator at 20±1°C, 60±5% relative humidity and a photoperiod of 16: 8 h (Light: Dark). Aphids were checked daily until mummification. This procedure was replicated 10 times on each host density (treatment) at each constant temperature.

Data Analysis

The type of functional response was determined using a logistic regression model. In this model, the proportion of hosts parasitized (N_a/N_0) as a function of initial host density (N_0) is the effective way to distinguish type of functional response (Juliano, 2001).

$$\frac{N_a}{N_o} = \frac{\exp(P_o + P_1N_o + P_2{N_o}^2 + P_3{N_o}^3)}{1 + \exp(P_o + P_1N_o + P_2{N_o}^2 + P_3{N_o}^3)}$$

Where N_a is the number of hosts parasitized, N_o is the initial host density and P_o, P_1, P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively. These parameters were estimated using maximum likelihood estimation method (Juliano, 2001). Linear coefficient (P_1) in type II and III functional response is negative and positive, respectively (De Clercq *et al.,* 2000; Juliano, 2001). A type II functional response rises at a decelerating rate to an upper asymptote (inversely density-dependent response), while the type III response is sigmoid (density dependent response) (Hassell, 1978).

After determining the type of functional response, searching efficiency (*a*) and handling time (T_h) parameters were estimated by random parasitoid equation (Rogers, 1972):

$$N_a = N_o\left[1 - \exp\left(\frac{aTP_t}{aT_hN_o}\right)\right]$$

Where N_a is the number of host parasitized, N_o is the number of host available, T is the total time of the experiment (=24 h), a is the instantaneous search rate, P_t is the number of parasitoid and T_h is the handling time. The parameters of the functional response equation (a and T_h) were estimated with nonlinear least squares regression. Statistical analysis of functional response was performed using the SAS software (SAS Institute, 2003). Statistical comparisons in different temperatures were carried out using SPSS 16.1 software with SNK tests (P < 0.05) (SPSS, 2004).

RESULTS

The mean parasitism rates of third-instar nymphs of *D. noxia* at various constant temperatures are shown in Table 1. The mean number of hosts parasitized increased with increasing host density at constant temperature of 15 (F= 35.361; df=5, 54; P<0.05), 20 (F= 312.365; df=5, 54; P<0.05), 25 (F= 167.886; df=5, 54; P<0.05), 30 (F= 193.434; df=5, 54; P<0.05) and 32.5°C (F= 96.368; df=5, 54; P<0.05). Host density had no significant effect on proportion of host parasitized at 10°C (F=2.169; df=5,54; P>0.05). The results of the current study indicated that the highest parasitism rate of

RWA was at 25°C (24.20±0.94) in density of 64 hosts. However, there was no significant difference between parasitism rates at 15, 20 and 25°C. There were significant differences between parasitism rates on hosts at various constant temperatures in host densities of 4 (F= 4.400; df= 5, 54; $P < 0.05$), 8 (F= 10.741; df= 5, 54; $P < 0.05$), 16 (F= 22.523; df= 5, 54; $P < 0.05$), 32 (F= 30.194, df= 5, 54; $P < 0.05$) and 64 (F= 40.768; df= 5, 54; $P < 0.05$), but there was no significant differences between parasitism rates in the host density of 2 (F= 2.377; df= 5, 54; $P > 0.05$). Temperature has been shown to have an effect on the number of hosts parasitized (Table 1).

Table 1. Mean (± SE) third instar nymphs of *Diuraphis noxia* parasitized by *Diaeretiella rapae* at various host densities at different constant temperatures.

Density	Mean hosts parasitized at different temperatures (°C)					
	10	15	20	25	30	32.5
2	0.90±0.28^{a}	1.60±0.22^{a}	1.70±0.15^{a}	1.60±0.16^{a}	1.40±0.16^{a}	1.10±0.23^{a}
4	1.50±0.40^{b}	3.10±0.28^{a}	3.20±0.29^{a}	2.80±0.33^{a}	2.30±0.26^{ab}	2.00±0.33^{ab}
8	1.90±0.59^{c}	5.60±0.60^{a}	5.70±0.42^{a}	5.10±0.31 ^{a}	4.10±0.23^{ab}	3.40±0.43^{b}
16	2.30±0.45^{d}	10.20±1.15^{ab}	11.20±0.65^{a}	9.70±0.42^{ab}	8.10±0.66^{bc}	6.50±0.50^{c}
32	2.80±0.73^{c}	16.50±1.82^{a}	17.60±0.54^{a}	18.40±1.30^{a}	15.10±0.567^{ab}	12.50±0.70^{b}
64	3.00±0.67^{d}	22.50±2.50^{a}	24.10±0.71^{a}	24.20±0.94^{a}	18.60±0.82^{b}	14.90±0.98^{c}

Values followed by different letters within rows are significantly different ($P < 0.05$).

Results of logistic regression to distinguish between type II and III responses are shown in Table 2. The negative values for the linear coefficients (P_1) indicated a type II functional response for *D. rapa*e at all temperatures tested. The functional response curve of *D. rapae* on different densities of RWA at different constant temperatures is illustrated in Fig. 1. The proportion of hosts parasitized by *D. rapae* declined with increasing host density. This suggests that, *D. rapae* exhibit a type II functional response. The slope of regression line at 10°C was very flat however, the regression at 10°C is still important because it shows that *D. rapae* has a very low parasitism rate at this temperature.

Table 2. Results of logistic regression analysis of the proportion of *Diuraphis noxia* third nymphs parasitized by *Diaeretiella rapae* at various constant temperatures.

Coefficients	Temperature (º C)					
	10	15	20	25	30	32.5
P_0	012±0.41	2.14±0.52	1.48±0.44	1.22±0.41	0.62±0.38	0.22±0.37
P_1	-0.19±0.07	-0.09±0.07	-0.05±0.06	-0.09±0.06	-0.07±0.06	-0.07±0.06
P_2	005±0.003	001±0.003	0.0004±0.002	0.003±0.002	0.002±0.001	0.002±0.001
P_3	-0.00004 ±0.000001	-0.00009 ±0.000001	-0.00002 ±0.000001	-0.00003 ±0.000001	-0.00002 ±0.000001	-0.00003 ±0.000001

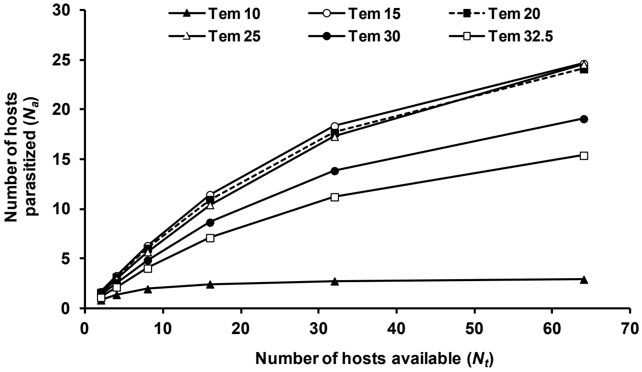

Fig. 1. Functional response of *Diaeretiella rapae* on different densities of third instar nymphs of *Diuraphis noxia* at various constant temperatures using the Rogers type II model.

The Rogers type II model was fitted for each temperature in order to estimate the searching efficiency and handling time. The searching efficiency (*a*), handling time (T_h), maximum attack rate (T/T_h) and efficiency parameter (a/T_h) at various constant temperatures are presented in Table 3. The temperature had significant effect on searching efficiency (F= 3.45; df= 5, 54; $P<0.05$). The searching efficiency (*a*), increased with increasing host density at various constant temperatures. The searching efficiency (*a*) was highest at 15°C and lowest at 10°C. The handling time varied in response to temperature (F=15.2738; df= 5, 54; $P<0.05$). The shortest and longest handling times were at 25°C (T_h= 0.657±0.056) and at 10°C (T_h= 7.683±1.219), respectively. The maximum attack rate ranged from 36.51 nymphs/24 h at 25°C to 3.124 nymphs/24 h at 10°C. The value of a/T_h indicated that *D. rapae* was more efficient against *D. noxia* at temperature between 15-25°C. The maximum value of a/T_h was observed at 15°C.

Fig. 2 shows effect of temperature and host density on the percentage parasitism by *D. rapae* in three-dimensional contour plot. Maximum percentage parasitism of third-instar nymphs of *D. noxia* by *D. rapae* occurred at 15, 20 and 25°C (Fig. 2).

Table 3. Estimates (± SE) of searching efficiency, handling time, maximum attack rate and a/T_h values of *Diaeretiella rapae* on third nymph instars of *Diuraphis noxia* at various constant temperatures.

Temperature (°C)	Searching efficiency (*a*) (h^{-1})	Handling time (T_h) (h)	Maximum attack rate (T/T_h)	a/T_h	R^2
10	$0.032±0.017^b$	$7.683±1.219^a$	3.12	0.004	0.721
15	$0.080±0.008^a$	$0.729±0.037^b$	32.94	0.110	0.955
20	$0.072±0.006^a$	$0.723±0.037^b$	32.22	0.099	0.969
25	$0.062±0.007^{ab}$	$0.657±0.056^b$	36.51	0.094	0.994
30	$0.047±0.005^b$	$0.866±0.064^b$	27.73	0.054	0.895
32.5	$0.036±0.005^b$	$1.058±0.106^b$	22.69	0.034	0.826

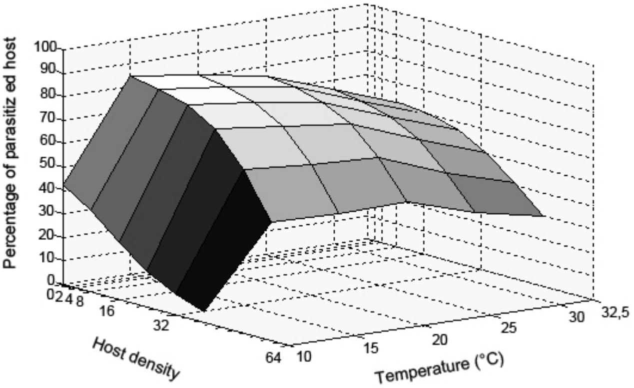

Fig. 2. Three-dimensional contour plot showing the effect of host density and temperature on the percentage parasitism by *Diaeretiella rapae*.

DISCUSSION

In this study, estimation of the functional response parameters (searching efficiency, handling time and maximum attack rate) of *D. rapae* were examined in laboratory experiments at six constant temperatures on six densities of third instar nymphs of *D. noxia* for 24 h. After a 24 h exposure period of the female parasitoid with the host aphids, to reduce the effects of temperature on mortality of *D. rapae*, the aphid nymphs were transferred into an incubator at 20±1°C (optimum temperature), 60±5% RH and a photoperiod of 16: 8 h (Light: Dark) until mummification. The results of this research indicated that temperature is an important factor affects searching efficiency and parasitism rate of *D. rapae*. A type II functional response was observed at all temperatures (because parasitization rate decreased monotonically with increasing host denity) and it was not affected by temperature. Type II functional response has also been reported for *D. rapae* on *M. persicae* (Yu *et al*., 1993), *D. noxia* (Bernal *et al*., 1994; Lester and Holtzer, 2002) and *B. brassicae* (Fathipour *et al*. 2006). Conversely, a type III functional response was reported for *D. rapae* on *L. erysimi* (Pandey *et al*., 1984; Abidi *et al*., 1987) and *S. graminum* (Dashti *et al*., 2010). Type II functional response have been reported in other species of the subfamily Aphidiinae, 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 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), *Aphidus colemani* Viereck and *Aphidius matricariae* (Haliday) on *Aphis gossypii* (Glover) (Zamani *et al*., 2006), *A. matricariae* on *Aphis fabae* Scopoli (Tahriri *et al*., 2007), and *Proan volucre* (Haliday) *on Sitobion avenae* (Fabricius) (Farhad *et al*., 2011). However, type III has previously been reported for *A. colemani* and *Lysiphlebus testaceipes* Cresson on *S. graminum* (Jones *et al*., 2003), *Trioxys* (*Binodoxys*) *indicus* Subba Rao and

Sharma on *A. craccivora* (Singh and Sinha, 1983), and *Trioxys pallidus* (Halliday) on *Chromoaphis juglandicola* (Kaltenbach) (Rakhshani *et al*., 2004)

Type of functional response among parasitic wasps may change under different experimental conditions, plant cultivar, parasitoid strain and host species (Bernal *et al*., 1994; Coll and Ridgway 1995; Messina and Hanks 1998; Lester and Holtzer, 2002; Fathipour *et al*. 2001).

The results of this research indicated that *D. rapae* could be more effective in reducing population of *D. noxia* between ambient temperatures of 15 and 25°C. According to Tazerouni (2011), the intrinsic rate of increase of *D. noxia* was higher at 15 and 20°C (0.142 and 0.220 day^{-1}, respectively) in comparison to lower and higher temperatures. *D. rapae* had also higher r_m-values at these temperatures, especially at 15°C (0.143 day^{-1}). Bernal and Gonzalez (1997) was also reported that *D. rapae* had high ability to increase population on *D. noxia* at 21.1 and 26.7°C (values r_m was estimated 0.182 and 0.202 days^{-1}, respectively). The activity of *D. rapae* adults reduced at lower (10°C) and higher temperatures (30 and 32.5°C). The optimal temperature for high rates of parasitization is different in the subfamily Aphidiinae. For example, *A. colemani* parasitizing *A. gossypii* on cucumber is able to parasitize 10.75 nymphs/24 h at 10°C and 31.25 nymphs/24 h at 30°C, but *A. matricariae* on *A. gossypii* is able to parasitize 12.82 nymphs/24 h at 10°C and 27.77 nymphs/24 h at 20°C (Zamani *et al*., 2006). The maximum estimated searching efficiency for *A. colemani* and *A. matricariae* was reported at 30°C (0.94 day $^{-1}$) and 25°C (0.687 day $^{-1}$), respectively (Zamani *et al*., 2006). The searching efficiency was highest at 15°C (0.08 h $^{-1}$). A lower handling time means higher numbers of hosts can be parasitized in a given time interval (Hassell, 1978). In the current study, handling time of *D. rapae* was lowest at 25°C (0.65 h). It is higher than those reported by Bernal *et al.,* (1994) (0.408 h) and Lester and Holtzer (2002) (0.024 h) for *D. rapae* on *D. noxia*. However, comparison handling time of *D. rapae* in our study with those of other studies is complicated by different factors, such as variability in origin of the parasitoid and host and experimental conditions (e.g., test arena, temperature). The shortest handling time for *A. colemani* and *A. matricariae* was 0.032 day at 30 °C and 0.036 day at 20°C (Zamani *et al*., 2006). However, the handling time for *A. colemani* and *A. matricariae* at 25°C was 0.043 (1.032 h) and 0.042 day (1.008 h), respectively (Zamani *et al*., 2006).

Functional responses may obtain important information to make decision in management programs (De Clercq *et al*., 2000; Mahdian *et al*., 2006; Li *et al*., 2007). The results of this research indicated that *D. rapae* has more ability to finding and parasitizing host (*D. noxia*) between temperatures of 15 and 25°C. Therefore we suggested *D. rapae* for augmentative release against the Russian wheat aphid at these temperatures in Iran. The activity of *D. rapae* adults reduced at lower (10°C) and higher temperatures (30 and 32.5°C). However, functional response studies in small laboratory arenas have been criticized as being unrepresentative of natural conditions (Kareiva, 1990; Bernal *et al*., 1994; Montoya *et al*., 2000) and should be interpreted with care. Information from this study will be used to develop a host-parasitoid model for *D. rapae* parasitizing *D. noxia*. This model should enhance our ability to develop biological control programs for RWA. However, for a comprehensive evaluation of the bio-control abilities of *D. rapae*, further field-based studies are needed.

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