

Research Article

Foraging Behavior of *Praon volucre* (Hymenoptera: Braconidae) a Parasitoid of *Sitobion avenae* (Hemiptera: Aphididae) on Wheat

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Host stage preference, functional response and, mutual interference of *Praon volucre* (Haliday) (Hym.: Braconidae) parasitizing the grain aphid, *Sitobion avenae* (Fabricius) (Hem.: Aphididae), were investigated under laboratory conditions. Host stage preference was evaluated at $25 \pm 1^\circ\text{C}$, $60 \pm 5\%$ relative humidity and a photoperiod of 16:8 h (L:D), under choice and no-choice tests. Functional response was done under five constant temperatures (10, 15, 20, 25, and 30°C), $60 \pm 5\%$ relative humidity and a photoperiod of 16:8 h. (L:D). *Praon volucre* parasitized all nymphal instars and adults of the grain aphid but strongly preferred to oviposit into second-instar nymphs in both choice and no-choice conditions. Results of logistic regression revealed a type II functional response for all temperatures tested. The handling time (T_h) and searching efficiency (a) were estimated using the Rogers equation. The maximum estimate of searching efficiency occurred at 15°C and 20°C (both $0.05 \pm 0.01 \text{ h}^{-1}$) and decreased to $0.01 \pm 0.01 \text{ h}^{-1}$ at $30 \pm 1^\circ\text{C}$. The minimum estimate of handling time was $1.02 \pm 0.11 \text{ h}$ at 25°C and increased to $5.31 \pm 0.82 \text{ h}$ at $30 \pm 1^\circ\text{C}$. The maximum rate of parasitism was 23.52 aphids/female/day at 25°C . With parasitoid density increasing from 1 to 8, the per capita searching efficiency decreased from 0.12 h^{-1} to 0.06 h^{-1} . The results suggested that *P. volucre* has the potential to be a biocontrol agent of *S. avenae*. However, evaluation of foraging behavior warrants further investigation under field conditions.

1. Introduction

The grain aphid, *Sitobion avenae* (Fabricius), is a cosmopolitan species [1]. This aphid causes direct damage by sucking plant sap and indirect damage by either excretion of honeydew or the transmission of viruses. It is found on many different species of Poaceae [2]. Chemical control has been the major tool for the control of aphids. However, biological control strategies are being increasingly applied because of rapid development of insecticides resistance in aphids and because of the effects of pesticides on natural enemies [3]. Parasitoids are important in biological control of cereal aphids [4], and several attempts have been made in introduction [5] and augmentative release of cereal aphid parasitoids [6]. Parasitoids are considered to be especially important in suppressing aphid populations earlier in the season because their appearances precede those of predators [7]. All members of the subfamily Aphidiinae (Hymenoptera: Braconidae) are important parasitoids of aphid species [8].

The genus *Praon* Haliday is one of the largest Aphidiinae genera with more than 50 described species worldwide [9]. *Praon volucre* (Haliday) is a parasitoid of *S. avenae* in Iran [10] Chile [11], Brazil [12], and Serbia [13].

Behavioral responses are one of the most important factors in selecting natural enemies in biological control programs [14]. Host-stage preference affects host-parasitoid population dynamics as the host's development status influences the development and reproduction of the parasitoid [15]. Functional response is the number of successfully attacked hosts as a function of host density [16]. It describes how a predator or parasitoid responds to the changing density of its host, and measuring it helps determine the expected effectiveness of natural enemies [17]. Functional response depends on handling time (T_h : the time that a natural enemy needs to parasitize a single host) and searching efficiency (a : the rate at which a parasitoid searches). Functional response is affected by different factors including temperature [18–20]. Mutual interference was

initially shown by Hassell and Varley [21]. Inverse density dependence between searching efficiency and parasitoid density is known as mutual interference [22]. The purpose of this research was to further investigate host stage preference, mutual interference among adult parasitoids, and the effect of temperature on functional response of *P. volucre*.

2. Materials and Methods

2.1. Plant and Insect Culture. Seeds of wheat (“Pishtaz” variety) were obtained from the Karaj Cereal Research Department of the Iranian Research Institute of Plant Breeding. The grain aphid and *P. volucre* were originally collected from the wheat fields in the campus of the Faculty of Agriculture, Tarbiat Modares University in Tehran, Iran, in October 2009. The aphids were reared on wheat seedlings grown in plastic pots (10.5 cm diameter and 9.5 cm height) and covered with transparent cylindrical plastic containers. The colony of aphid parasitoid was reared on *S. avenae* colonies for 3-4 generations before the parasitoids were used in the experiments. The aphid and its parasitoid colonies were maintained in a growth chamber at $25 \pm 1^\circ\text{C}$, $60 \pm 5\%$ relative humidity and a photoperiod of 16:8 h (Light:Dark). All experiments were carried out using seedlings of wheat about 15 cm in height.

2.2. Host Stage Preference. Host-stage preference was determined by both choice and no-choice experiments. In the no-choice tests, 50 individual aphids of a single stage (first, second, third, and fourth instar or adult) were released on a wheat seedling and were exposed to a pair of 1-day-old male and female parasitoids. Our preliminary study showed that the maximum parasitism rate was 15 aphids per female parasitoid per day (unpublished data). To avoid superparasitism, we used 50 aphids per female parasitoid (e.g., more than three times maximum parasitism rate). After 24 h, the parasitoids were removed. The aphids were reared on wheat seedlings until mummies appeared. In the choice tests, all instars were established on a wheat seedling (10 aphids from each instar on each seedling) and were then exposed to a pair of 1-day-old male and female parasitoids for 24 h. Then each instar was held separately until the aphids mummified. Both the choice and the no-choice preference tests were replicated 10 times in cylindrical plastic containers (5 cm diameter and 15 cm height) in the same conditions as above. A streak of honey-water solution (20%) was placed on wheat leaves as a source of carbohydrates and water for the adult parasitoids. Data were checked for normality prior to analysis. The data were analyzed using one-way ANOVA [23]. If significant differences were detected at $P < 0.05$, means were compared using the Student-Newman-Keuls (SNK) post hoc test.

2.3. Functional Response. The effect of host density on parasitism was investigated at temperatures of 10, 15, 20, 25, and $30 \pm 1^\circ\text{C}$, $60 \pm 5\%$ relative humidity and a photoperiod of 16:8 h (Light:Dark). Second-instar nymphs, either 2, 4, 8, 16, 32, or 64 of them, were placed on a wheat seedling (15 cm in height) and placed into a cylindrical plastic container (5 cm diameter and 15 cm height). The top of

the container was covered with fine nylon mesh, and the aphids were exposed to a pair of 1-day-old male and female parasitoids for 24 h. Honey-water solution (20%) was provided for adult parasitoids. Host feeding was not determined in this research. The aphids were reared on the plants until mummies were formed. Each aphid density at each temperature was replicated 10 times. To determine the type of functional response, the data were fitted to the logistic regression [19, 24, 25]

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

P_0 , P_1 , P_2 , and P_3 are the intercept, linear, quadratic and cubic coefficients, respectively. N_a is the number of hosts parasitized, N_0 is the initial host density, and N_a/N_0 is the proportion of total aphids parasitized. A significant negative or positive linear coefficient (P_1) of the logistic regression model indicates type II or III, respectively [24]. After defining the type of functional response, the handling time (T_h) and searching efficiency (a) of a type II response were estimated using Rogers equation [26] as follows:

$$N_a = N_0 \left[1 - \exp\left(-\frac{aTP_t}{1 + aT_h N_0}\right) \right], \quad (2)$$

N_a is the number of host parasitized, N_0 is the initial host density, T is the duration of the experiment (= 24 h), a is searching efficiency, T_h is handling time and P_t is the number of parasitoids. Handling time (T_h) and searching efficiency (a) were estimated using non-linear regression and SAS software [23].

2.4. Mutual Interference. In this experiment, 120 second-instar nymphs of *S. avenae* were placed on wheat seedlings and exposed to groups of 2, 4, 6, and 8 one-day-old mated females. After 24 h, the parasitoids were removed from the cages (5 cm diameter and 15 cm height), and the aphids were held at $20 \pm 1^\circ\text{C}$, $60 \pm 5\%$ relative humidity and 16:8 h (Light:Dark) photoperiod until mummies were produced. Each parasitoid density was replicated 10 times. The per capita searching efficiency (a) of the parasitoids at different parasitoid densities was calculated according to the Nicholson equation:

$$a = \left(\frac{1}{PT}\right) \ln\left(\frac{N_t}{(N_t - N_a)}\right), \quad (3)$$

N_t is the total number of hosts available (= 120), N_a is the total number of hosts attacked, P_t is the number of parasitoids, and T is the duration of the experiment (= 24 h). Searching efficiency was fitted to a linear regression by the least square method, using the inductive model of Hassell and Varley [21]:

$$a = QP^{-m}, \quad \text{or} \quad \log a = \log Q - m \log P \quad (4)$$

a is the searching efficiency of the parasitoid, Q is the quest constant (intercept of the regression line), and m is the mutual interference constant (slope of the regression line). In

TABLE 1: Maximum likelihood estimates from logistic regressions of proportion of different densities of *Sitobion avenae* by *Praon volucre* at various constant temperatures.

Temperatures (°C)	Parameters			
	Intercept (P_0)	Linear (P_1)	Quadratic (P_2)	Cubic (P_3)
10	0.650 ± 0.38	-0.217 ± 0.061	0.007 ± 0.002	-0.00008 ± 0.0001
15	0.48 ± 0.37	-0.016 ± 0.057	-0.001 ± 0.002	0.000018 ± 0.0001
20	2.58 ± 0.496	-0.253 ± 0.069	0.006 ± 0.002	-0.00006 ± 0.0001
25	1.809 ± 0.426	-0.207 ± 0.062	0.005 ± 0.002	0.00005 ± 0.0001
30	-1.167 ± 0.448	-0.0004 ± 0.07	-0.001 ± 0.001	0.000019 ± 0.0001

this model, m includes only the component of interference due to behavioral interactions between parasitoids [27]. Excel software was used to draw figures.

3. Result and Discussion

3.1. Host Stage Preference. *Praon volucre* parasitized all nymphal instars and adults of the grain aphid but strongly preferred to oviposit into second instar nymphs in both choice preference test ($F = 3.38$, d.f. = 4, 49, $P < 0.05$) and no-choice preference test ($F = 7.87$, d.f. = 4, 49, $P < 0.01$) (Figure 1). *Aphidius rhopalosiphi* De Stefani-Perez preferred second- and third-instar nymphs of cereal aphids for oviposition [28]. Our finding was consistent with *Diaeretiella rapae* (M'Intosh) preferring second-instar nymphs of *Brevicoryne brassicae* (L.) for oviposition [29]. By contrast, *Aphidius matricariae* (Haliday) preferred to oviposit into third-instar nymphs of *Aphis fabae* (Scopoli) [30]. Hagvar and Hofsvang [31] demonstrated the parasitism of an aphid nymphal instar influenced the development and fecundity of the aphids as well as their parasitoids. The parasitoids that parasitized first-instar nymphs of aphids did not mature. *Aphidius colemani* Viereck females, for example, prefer second instar nymphs of *M. persicae*, which may maximize fitness gain [32]. It is generally assumed that second- and third-instar nymphs of aphids are preferred by parasitoids because of physiological characteristics. Young host stages provide inadequate food for the successful development of offspring, whereas mortality risk of parasitoid progeny from encapsulation in young host stages is less than in late stages [33]. However, the host stage preference is flexible, and it is influenced by several factors, such as experimental conditions [34], host behavior (particularly aphid defense), and availability of each instar in the field [35]. Host-stage preference is also affected by test duration and host densities [36]. It is well known that host stage selection can affect considerably the population growth of both host and parasitoid and, therefore, can have a definite effect on whether a pest population can be controlled successfully by the parasitoids [31].

3.2. Functional Response. Significant negative linear coefficients of the logistic regression model indicated a type II functional response at all temperatures tested (Table 1, Figure 2). The type of functional response was not affected by temperature, indicating that *P. volucre* is well adapted to

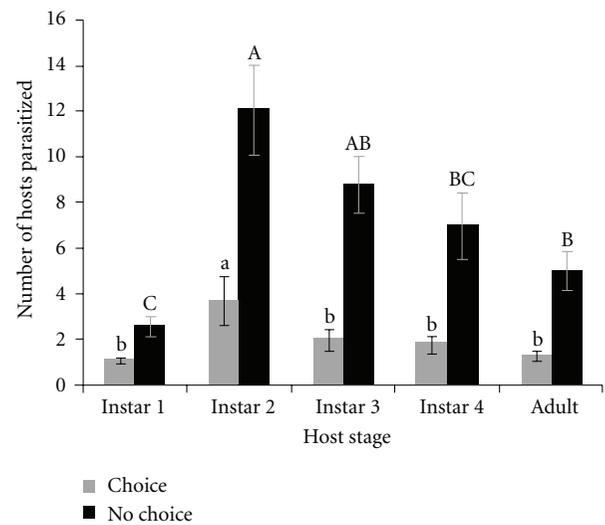


FIGURE 1: Host-stage preference of *Sitobion avenae* parasitized by *Praon volucre* in choice (□) and no-choice (■) tests.

temperature changes. The ability of *P. volucre* to parasitize grain aphid over a broad range of temperatures makes it as a good candidate for biological control of grain aphid. The proportion of hosts parasitized by *P. volucre* decreased with increasing host density (Figure 2). Searching efficiency was the highest at 15°C ($0.05 \pm 0.01 \text{ h}^{-1}$), and 20°C ($0.05 \pm 0.01 \text{ h}^{-1}$) and was the lowest at 30°C ($0.01 \pm 0.01 \text{ h}^{-1}$) (Table 2). Handling time decreased with an increase in temperature up to 25°C, then increased at 30°C. Results from this study suggest that this parasitoid could be more effective in reducing populations of *P. volucre* at 20–25°C than at higher and lower temperatures. The lowest handling time was observed at 25°C ($1.02 \pm 0.11 \text{ h}$). The maximum estimate of parasitism (T/T_h) was at 25°C (23.52 nymphs parasitized/female/day) (Table 2).

Handling time is defined as the time spent handling the host, parasitizing the host, and also the time spent cleaning and resting. The effect of handling time is to reduce the time available for search for other hosts [37]. The type II functional response is the most frequent in insects [33]. *Aphidius uzbekistanicus* (Luzhetskii) showed a type II functional response to *Metopolophium dirhodum* (Walker) [38]. Also type II functional response has been reported by Zamani et al. [39] for *A. matricariae* and *A.*

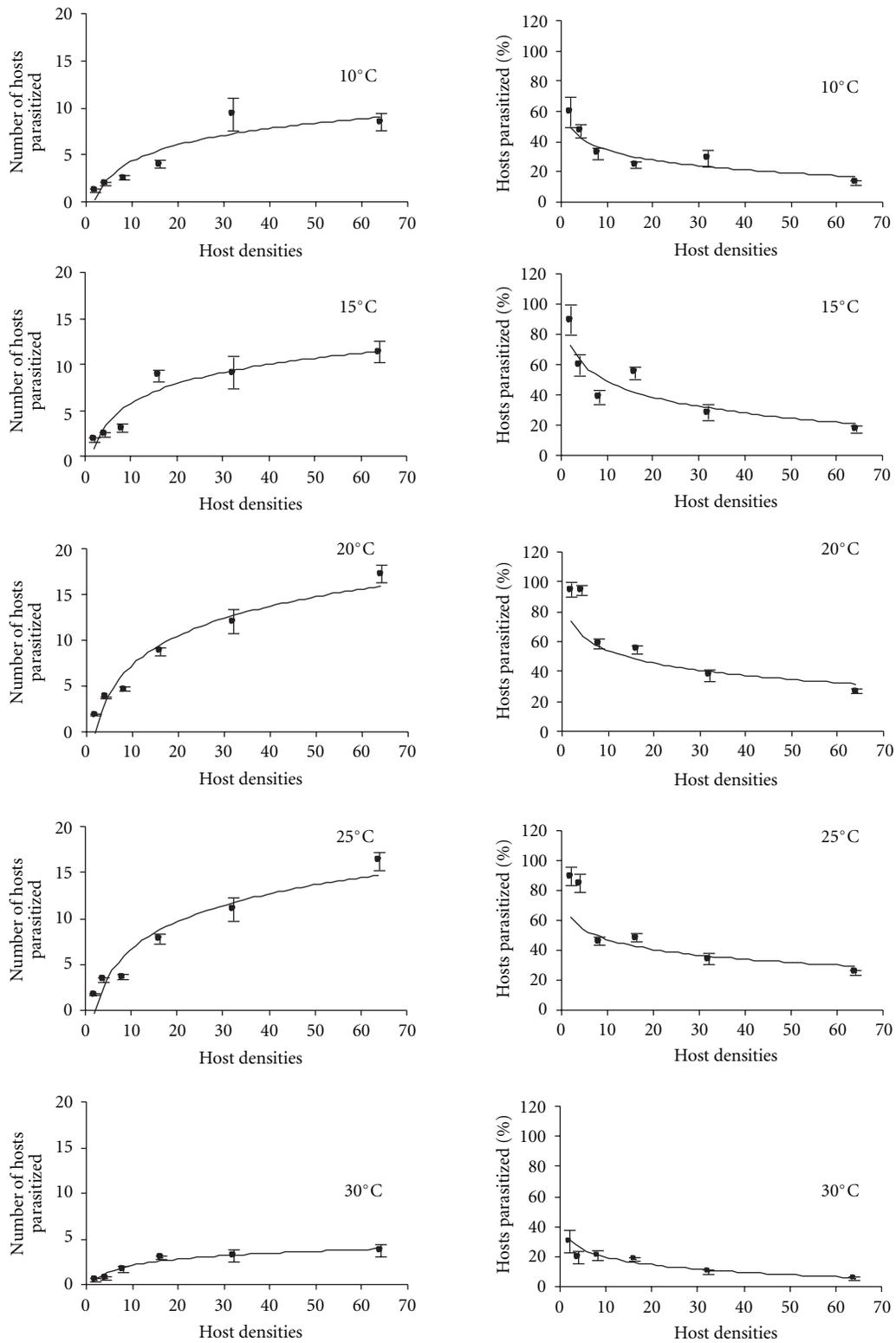


FIGURE 2: Type II-functional response of *Praon volucre* on different densities of second-instar nymphs of *Sitobion avenae* at various constant temperatures.

TABLE 2: Mean \pm SE (minimum-maximum) estimates of handling time (T_h), searching efficiency (a), and maximum rate of parasitism (T/T_h) of *Praon volucre* on *Sitobion avenae*.

Parameters	Temperatures ($^{\circ}$ C)				
	10	15	20	25	30
Handling time (T_h)	1.95 \pm 0.34 (1.25–2.65)	1.78 \pm 0.21 (1.34–2.22)	1.06 \pm 0.09 (0.86–1.25)	1.02 \pm 0.11 (0.79–1.26)	5.31 \pm 0.82 (3.65–6.96)
Searching efficiency (a)	0.02 \pm 0.001 (0.01–0.04)	0.05 \pm 0.001 (0.02–0.08)	0.05 \pm 0.001 (0.03–0.06)	0.03 \pm 0.001 (0.02–0.05)	0.01 \pm 0.001 (0.00–0.02)
Maximum rate of parasitism (T/T_h)	12.30	13.48	22.64	23.52	4.51
Coefficient of determination (r^2)	0.79	0.84	0.94	0.93	0.75

colemanni on *Aphis gossypii* Glover, for *A. matricariae* on *A. fabae* [30], and for *D. rapae* on *B. brassicae* [29]. *Praon* near *occidentale* showed a type II functional response on *Macrosiphum euphorbiae* (Thomas) at 18, 20 and 25 $^{\circ}$ C [40]. Searching efficiency was the highest at 18 $^{\circ}$ C (0.1081 h $^{-1}$) and handling time was shortest at 25 $^{\circ}$ C (4.89 h). The maximum number of parasitized aphids was 4.9 at 25 $^{\circ}$ C, which was much lower than that of obtained in the present study (23.52 at 25 $^{\circ}$ C). By contrast, Stilmant [41] showed a type III functional response for *P. volucre*, *A. rhopalosiphi*, and *A. ervi* on *S. avenae*. The handling time, instantaneous attack rate, and maximum number of hosts parasitized by *P. volucre* were estimated as 0.004 day, 0.493 day $^{-1}$ and 42.3 nymphs parasitized/parasitoid/day, respectively [41]. The difference between these values may be related to the origin of the populations and different experimental conditions. Type III functional response has been reported for *Trioxys pallidus* (Haliday) on *Chromaphis juglandicola* (Kaltenbach) [42], and also for *A. colemanni* and *Lysiphlebus testaceipes* (Cresson) on *Schizaphis graminum* (Rondani) [43].

The functional response is affected by the experimental conditions, age of parasitoids, time of exposure, and temperatures [44]. *Aphidius uzbekistanicus* showed a type III response when parasitizing third-instar nymphs of *Hyalopteroides humulis* Walker but a type II response when parasitizing *M. dirhodum* [38]. According to Hofsvang and Hågvar [45], *Ephedrus cerasicola* Stary exposed to hosts for 1, 6 and 24 h showed type II, type I, and type II functional responses, respectively. *Lysiphlebus testaceipes* showed type II and type III functional responses at 20 $^{\circ}$ C and 28 $^{\circ}$ C, respectively [17]. In natural field conditions natural enemies can move freely to patches with high densities of hosts, but, in laboratory conditions, natural enemies are forced to remain in a patch for a fixed length of time; therefore, under laboratory conditions the type III functional response is less common than the type II [46]. The reason why type III response is rare in invertebrate predators and parasitoids may be caused by experimental procedures in which the numbers of prey or hosts at low densities is higher than what can be expected in fields [47].

3.3. Mutual Interference. With increasing parasitoid densities from 1 to 8, the per capita parasitism decreased significantly

TABLE 3: Mean \pm SE per capita parasitism and searching efficiency of *Praon volucre* on *Sitobion avenae*.

Parasitoid densities	Per capita parasitism	Per capita searching efficiency (a)
1	13.6 \pm 0.93 ^a	0.1206 \pm 0.008 ^a
2	9.80 \pm 0.38 ^b	0.0893 \pm 0.003 ^b
4	8.65 \pm 0.08 ^b	0.0850 \pm 0.001 ^b
6	6.51 \pm 0.15 ^c	0.0658 \pm 0.001 ^c
8	5.72 \pm 0.06 ^c	0.0601 \pm 0.001 ^c

from 13.6 \pm 0.93 to 5.72 \pm 0.06 ($F = 46.14$, d.f. = 4, 49, $P < 0.01$) (Table 3). Accordingly, the per capita searching efficiency (a) decreased significantly from 0.12 \pm 0.01 to 0.06 \pm 0.01 as parasitoid density increased from 1 to 8 ($F = 28.80$, d.f. = 4, 49, $P < 0.01$). The mean numbers of hosts parasitized increased significantly as the parasitoid density increased ($F = 351.06$, d.f. = 4, 49, $P < 0.01$) (Table 3). The equation of linear regression between the logarithm of per capita searching efficiency (a) and the logarithm of parasitoid density (P) was $\log a = -0.3164 \log P - 0.9246$ (Figure 3). The slope of the regression line (the interference coefficient) was -0.3164 . This negative value shows an inverse relationship between parasitoid density and per capita searching efficiency. The negative relationship between per capita searching efficiency and parasitoid density was also documented in *D. rapae* on *B. brassicae* [29], and *Lipaphis erysimi* (Kaltenbach) [48, 49]. This reaction refers to intraspecific competition in the parasitoids. In addition, high parasitoid density causes a higher proportion of male progeny, probably because the females laid unfertilized eggs [50]. The significant reduction of host parasitization per parasitoid with increasing parasitoid density suggests that interference amongst parasitoids also increased at higher parasitoid density. This is probably due to a closed experimental arena and limited time for parasitization and a high probability of mutual interference [30]. In nature, parasitoids may be more attracted to patches of high host density than to patches of low host density [51]. Aggregation of parasitoids in high host density patches increases the probability of encounters between parasitoid individuals. The effect of

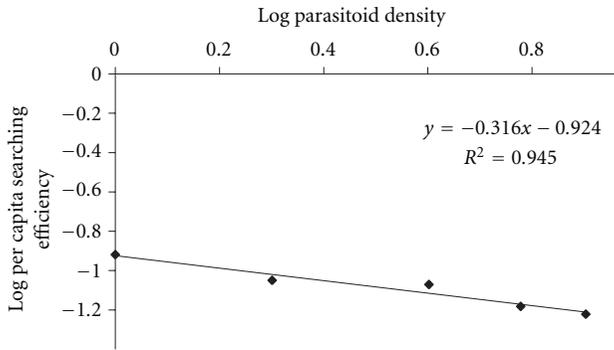


FIGURE 3: Regression line in mutual interference of *Praon volucre* on second-instar nymphs of *S. avenae*.

these encounters (i.e., mutual interference) is to reduce parasitoid searching efficiency and searching time [37]. Accordingly, in our study, the searching efficiency of *P. volucre* decreased as the parasitoid density increased (Table 3).

This study provides information on host-parasitoid interactions, which are helpful in management of *S. avenae*. However, field-based studies are needed to determine *P. volucre*'s impact on *S. avenae* and to achieve more realistic results.

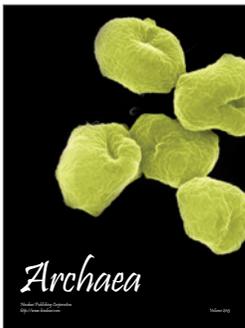
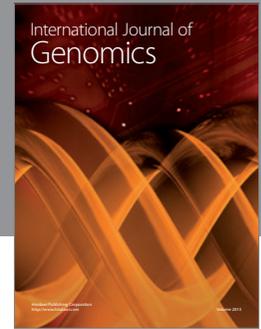
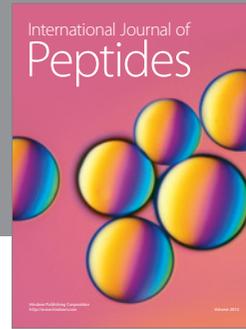
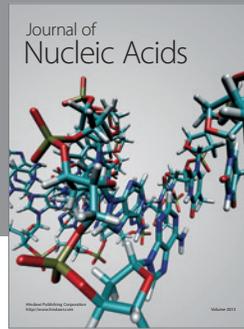
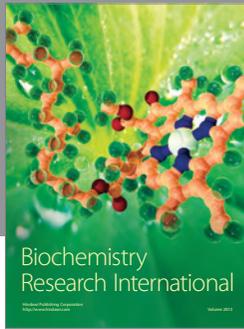
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