

Host plant effect on functional response and consumption rate of *Episyrphus balteatus* (Diptera: Syrphidae) feeding on different densities of *Aphis gossypii* (Hemiptera: Aphididae)

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Abstract: One of the most important predator-prey interactions is functional response which its type and parameters are affected by different factors including host plant characteristics. In this research, the influence of leaf surface on functional response and prey consumption rate of third instar larvae of the *Episyrphus balteatus* (De Geer, 1776) (Diptera: Syrphidae) to third instar nymphs of *Aphis gossypii* Glover (Hemiptera: Aphididae) were studied on sweet pepper and cucumber leaves. The results demonstrated that leaf surface of host plants; different prey densities and their interaction had significant effects on the numbers of prey killed by a predator. Logistic regression indicated type III functional response on both host plant leaves. The values of b constant were 0.00231 and 0.00351h⁻¹ while handling time (T_h) estimates were 0.14 h and 0.095 h on cucumber and sweet pepper leaves respectively. Moreover, plant leaves and different prey densities had significant effect on the prey consumption rate and voracity of predator. The maximum voracity values reached were 180.73 ± 7.71 and 282.25 ± 11.71 nymphs on cucumber and sweet pepper leaves respectively. These results emphasize on the importance of physical traits of host plant surface on the performance and searching efficiency of natural enemies that should be considered for optimizing their application in aphid biological control.

Keywords: Physical traits, trichomes, predation rate, handling time, syrphids

Introduction

E. balteatus is one of the most important commercial flies released against different aphid species especially in greenhouses since 1990 (van Lenteren, 2012). The larvae of this species have been known as predator of more than 100 species of aphids worldwide (Sadeghi and Gilbert, 2000) and its predation has been investigated on some species like cotton aphid,

Aphis gossypii Glover (Poligui *et al.*, 2011), *Myzus persicae* Sulzer (Hemiptera: Aphididae) (Verheggen *et al.*, 2009) and *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) (Putra and Yasuda, 2006). Several studies have shown high performance of *E. balteatus* especially concerning different species of cereal aphids, *M. persicae* Sulzer on tobacco and *Brevicoryne brassicae* L. (Hemiptera: Aphididae) on *Brassica* plants (Hindayana, 2001). Cotton aphid or melon aphid, *A. gossypii* is one of the most serious greenhouse pests that has a broad host range. It attacks more than 700 host plant species and transmits important viruses like

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potyviruses (Blackman and Eastop, 2000; Capinera, 2001).

Terrestrial communities based on living plants are combined of at least three trophic levels including host plants, herbivores and their natural enemies. In these complex systems, plants because of their extensive cover have important impacts not only on herbivores but also on the natural enemies and their interactions. These effects may be physical (such as trichomes, tissue roughness) or chemical (such as toxins and digestibility reducers) (Price *et al.*, 1980; Schoonhoven *et al.*, 2005). One of the most important predator-prey interactions is functional response. Functional response is a short behavioral predator (parasitoid)-prey (host) interaction that gives insights into predaceous capacity of natural enemies and enhances predictability of biological control (Houck and Strauss, 1985). Among the criteria used for evaluating the efficiency of natural enemies, are searching efficiency and handling time that both parameters are measured by the response of predator (or parasitoid) to increasing prey (or host) density (i.e. functional response) (Holling, 1959, 1961). Different factors may influence predator searching pattern and consequently change functional response type or parameters values. These factors include temperature (Enkegaard, 1994; Mohaghegh *et al.*, 2001; Gilioli *et al.*, 2005; Moezipour *et al.*, 2008; Moayeri *et al.*, 2013), experimental unit complexity (Madadi *et al.*, 2011), feeding history (Castagnoli and Simoni, 1999), prey (host) type (Donnelly and Phillips, 2001; Hoddle, 2003; Allahyari *et al.*, 2004) and predator (parasitoid) age and life stages (Carneiro *et al.*, 2010; Farhadi *et al.*, 2010).

Host plant surface properties such as trichome density and shape may affect the search pattern and foraging behavior of predators and consequently by changing the searching efficiency may be effective on the functional response of the predators. These effects have been addressed by some authors (e.g. Messina and Hanks, 1998; Krips *et al.*, 1999; DeClercq *et al.*, 2000; Madadi *et al.*,

2007; Mahdian *et al.*, 2007; Karami Jamur and Shishehbor, 2012).

Despite much literature dealing with the effect of plant physical traits on searching efficiency of predators, the effect of leaf surface physical traits on predation rate of *E. balteatus* has not been addressed so far. Therefore, the goal of this study was to investigate the effect of two leaf surfaces on predation efficiency and voracity of *E. balteatus* against *A. gossypii*, one of the most important pests of vegetable crops.

Materials and Methods

Insects and plant rearing

E. balteatus larvae were collected from apricot orchards (Hamedan province, N 34° 78', E 48° 48' and 1825m altitude and Doroud, Lorestan Province, N 33° 31', E 49° 00', and 1522.25 altitude) infested by mealy plum aphid, *Hyalopterus arundinis* F. The collected larvae were fed on cotton aphid ad libitum daily. Pupae were placed in muslin net covered cage (30 × 60 × 60 cm). When adults emerged, they were fed on canola pollen and honey-water solution (10%) as supplementary diet provided within the cage. Adults' diet changed every day. Females were stimulated to lay more eggs by placing sweet pepper seedlings infested with cotton aphid inside the cage. Eggs were collected and individually placed on sweet pepper leaves in Petri dishes (8 cm diameter).

All rearing and experimental procedures were done in a growth chamber under 22 ± 1 °C, 60 ± 10% R. H. and 16: 8h L: D photoperiod.

All experiments were carried out on two host plants; cucumber (*Cucumis sativus* L. var. Negin) and sweet pepper (*Capsicum annuum* L. var. Enzazaden). These host plants usually get infested with cotton aphid as an important pest of greenhouse vegetable crops. Furthermore, the plant species differ, among other things, for the number of trichomes on their surfaces, i.e. sweet pepper leaf is smooth and void of trichomes, while cucumber leaf has sparse straight trichomes (Fig. 1).

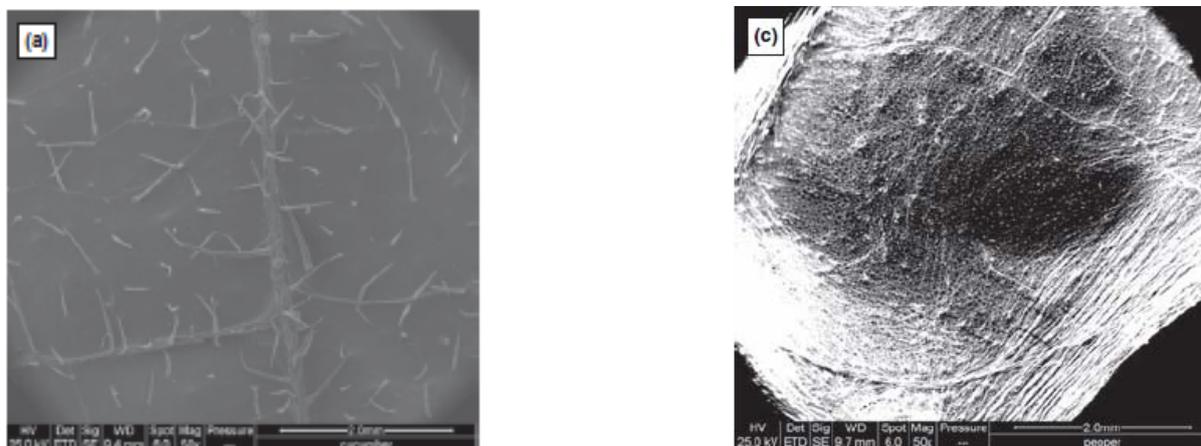


Figure 1 Scanning electron photo of (a) cucumber and (c) sweet pepper leaf surface (Madadi *et al.*, 2007).

The experimental unit consisted of a mature cucumber and sweet pepper leaf (leaf area approximately 47.1 and 42.85 cm², respectively). Leaves were placed up side down on moistened filter paper and cotton wool to maintain leaf freshness.

Functional response experiment

Ten different densities including 4, 8, 16, 32, 64, 100, 180, 250, 350 and 520 of third instar nymphs of *A. gossypii* were placed randomly on each leaf. The highest density was used only for sweet pepper. A third instar *E. balteatus* larva was introduced in each arena. This is the most voracious predatory stage of all larval stages (Putra and Yasuda, 2006). Then, experimental units were placed in growth chamber at 22 ± 2 °C, 60 ± 10% RH and under a 16:8h L: D photoperiod. Larvae were starved prior to starting the experiment for six hours. The number of replicates was 12 for all densities on each of the two host plant leaves. Prey killed were not replaced during the experiments. After 24h., the predators were removed and the number of dead and live prey were recorded. Mortalities of aphids without predators were recorded at the same conditions.

Data analysis

The GLM procedure was used to compare the effect of host plant leaves, different prey densities

and their interaction on the number of aphids eaten by the predator (SAS Institute Inc., 2004).

The general method for analyzing the functional response includes two main steps: model selection and parameters estimation.

Model selection involves using a logistic regression of proportion of killed prey versus initial number of prey to define the general shape of the functional response. This involves fitting a polynomial function (1) (Juliano, 2001):

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

Where N_a is the number of prey eaten, N_0 is the initial number of prey offered, and P_0 , P_1 , P_2 and P_3 are the intercept, linear, quadratic and cubic coefficients to be estimated respectively.

Negative linear parameter indicates type II response, whereas a positive linear parameter indicates type III functional response (CATMOD procedure, SAS Institute Inc., 2004) (Juliano, 2001).

Non-linear least square regression has been used for estimating the parameters of functional response, i.e. attack rate (instantaneous searching rate (a)) and handling time (T_h) (NLIN procedure, SAS Institute Inc. 2004) based on Holling's disc equation (2) (Holling, 1959)

(2) Holling's disc equation

$$N_a = \frac{aNT}{(1 + aNT_h)}$$

For type III functional response:

$$N_a = N_0 \{1 - \exp[(d + bN_0)(T_h N_e - T) / (1 + c N_0)]\}$$

where T is the total time available (here T = 24 hrs.), N₀ is the initial number of prey, N_a is the number of prey killed and b, c and d are constants.

Aphid mortalities are corrected by Abbott equation (Abbott, 1925) as follows:

$$\% \text{ Control} = \frac{x-y}{x} \times 100$$

which x and y are the percent living in the control and treatment respectively.

Obtained parameters (attack rate and handling time) were compared by using t-tests (SAS Institute Inc. 2004).

Maximum number of aphids killed (T/T_h) was calculated and the voracity of *E. balteatus* was obtained using equation 4 (Soares *et al.*, 2003):

$$(4) V_0 = (A - a_{24}) ra_{24}$$

where V₀ and A are the numbers of aphids eaten and available, a₂₄ is the number of aphids

alive after 24 h and ra₂₄ is the ratio of aphids alive after 24 h. in the control

Obtained data were analyzed by non-parametric tests if they did not meet the normal distribution requirements.

Results

The results showed that host plant species (F = 126, df = 1, 209, P < 0.0001), prey density (F = 608.6, df = 9, 209, P < 0.0001) and their interaction (F = 44.79, df = 8, 209, P < 0.0001) had a significant influence on the predation of aphids by *E. balteatus*.

The logistic regression analysis showed that third instar larvae of *E. balteatus* exhibited type III functional response on the two host plant leaves because the linear coefficient was positive (Table 1, Figs. 2 and 3)

Table 2 shows estimated parameters of functional response.

Table 1 Logistic regression analyses of the proportion of third instar nymphs of *Aphis gossypii* eaten by third instar larvae of *Episyrphus balteatus* on two host plants.

Host plant	Parameter	Estimate	SE	X ² value	P value
Cucumber	Constant	1.0535	0.0852	152.85	< 0.0001
	Linear	0.00901	0.000888	103.18	< 0.0001
	Quadratic	-0.00004	2.034E-6	333.51	< 0.0001
Sweet pepper	Constant	2.3889	0.1021	547.88	< 0.0001
	Linear	0.00347	0.000665	27.21	< 0.0001
	Quadratic	-0.00002	9.687E-7	308.74	< 0.0001

Table 2 Parameters estimated by Holling's disc equation and corresponding asymptotic 95% confidence intervals, indicating functional response of third instar larvae of *Episyrphus balteatus* to densities of third instar nymphs of *Aphis gossypii* on two host plant leaves.

Host plant	Parameter	Estimate ± SE	Approximate confidence limit	R ²
Cucumber	b	0.00231 ± 0.0005	0.00132-0.003	0.96
	T _h	0.1404 ± 0.004	0.1321-0.149	
Sweet pepper	b	0.00351 ± 0.0014	0.000719-0.006	0.97
	T _h	0.0953 ± 0.0027	0.0899-0.1006	

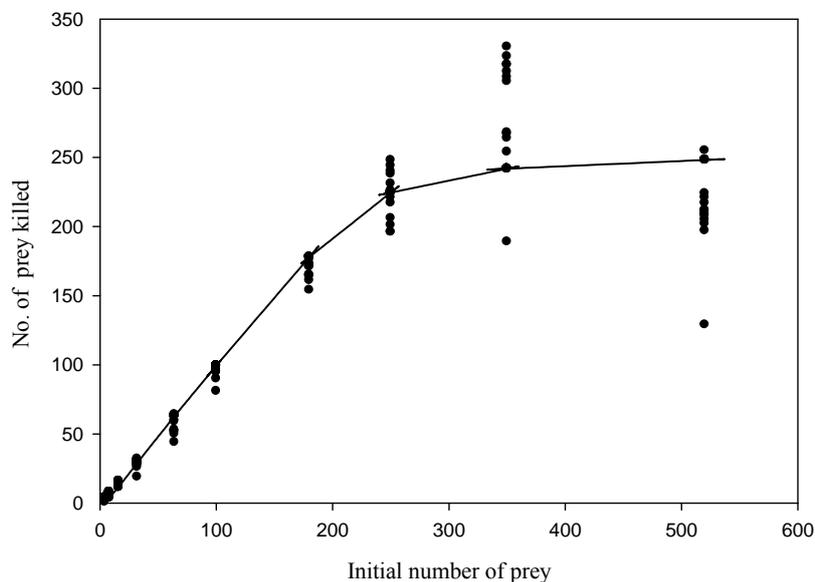


Figure 2 Functional response of third instar larvae of *Episyrrhus balteatus* to *Aphis gossypii* nymphs on sweet pepper. The symbols represent observed values while line shows fitted model.

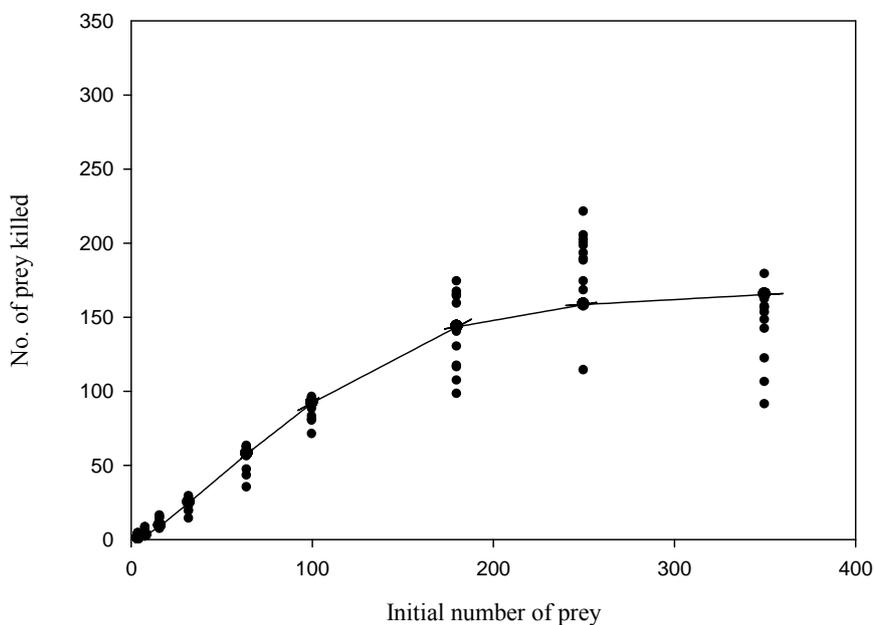


Figure 3 Functional response of third instars larvae of *Episyrrhus balteatus* to *Aphis gossypii* nymphs on cucumber. The symbols represent observed values while line shows fitted model.

Here both c and d are equal to zero, so search rate (a) is a function of N_0 , i.e. $a = b N_0$ (Juliano, 2001).

It was revealed that handling time was affected by plant surface, or host plant significantly (T-test, $t = 25.99$, P-value < 0.001). The theoretical maximum number of *A. gossypii* nymphs eaten by a third instar larva of *E. balteatus* was 170.94 and 251.84 nymphs per day on cucumber and sweet pepper respectively.

Voracity

The number of prey eaten by third instar larvae of *E. balteatus* was increased significantly with different prey densities on two host plant leaves ($F = 219.18$, $df = 8, 99$, P-value < 0.0001) for cucumber and ($F = 434.17$, $df = 9, 110$, P-value < 0.0001) for sweet pepper. The highest numbers were 180.73 ± 7.71 prey on cucumber and 282.25 ± 11.71 prey on sweet pepper respectively. Their values were very close to theoretical maximum attack rate. Moreover, physical traits of plant leaves significantly influenced voracity of *E. balteatus* on each density except for 64 aphid nymphs (Kruskal - Wallis test, P-value < 0.0001) and then decreased on both host plants (Table 3).

Table 3 Voracity (mean \pm SE) of third instar larvae of *Episyrphus balteatus* on cucumber and sweet pepper leaves

Initial prey density (N_0)	Cucumber	Sweet pepper
4	2.68 ± 0.13	3.66 ± 0.18
8	5.42 ± 0.49	6.65 ± 0.38
16	10.47 ± 0.87	14.63 ± 0.42
32	22.60 ± 1.15	27.58 ± 1.10
64	53.80 ± 2.55	55.22 ± 1.71
100	85.57 ± 2.70	92.99 ± 1.88
180	137.69 ± 7.52	164.91 ± 2.16
250	180.73 ± 7.71	218.78 ± 5.26
350	143.21 ± 7.65	282.25 ± 11.71
520	-	203.21 ± 7.97

Discussion

The results suggest that the physical traits of the plant surface can affect on functional response and predation rate of *E. balteatus* feeding on *A. gossypii* but not on the type of functional response. Unlike De Clercq *et al.*, (2000) who indicated that *Podisus nigrispinus* Dallas (Hemiptera: Pentatomidae) exhibited different responses to densities of fourth instar *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae) on various plant species, type III functional response was the best fit for *E. balteatus* on both host plants. Findings of the current study are consistent with those of Tenhumberg (1995) who found a type III functional response for *E. balteatus* on *Sitobion avenae* (F.) (Hemiptera: Aphididae) and *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae) in caged winter wheat within the field.

Other researchers reported different type of functional response for *E. balteatus*. Surprisingly, Putra and Yasuda (2006) demonstrated that the third instar larvae of *E. balteatus* showed linear functional response to the *A. pisum* and *Aphis craccivora* Koch. (Hemiptera: Aphididae). Additionally, Jalilian *et al.*, (2011) showed that *E. balteatus* exhibited type II functional response on *M. persicae*. The estimated searching efficiency and handling time of *E. balteatus* to green peach aphid were 0.0677/h and 0.316h, respectively (Jalilian *et al.*, 2011) that were higher than our results. The discrepancy of results with those studies may be due to different test designs. They used simple Petri dish arena and in latter study each treatment was replicated only six times. van Lenteren and Baker (1976) attributed the higher incidence of type II functional response to experimental arena size that is too small to provide real encounter rate of predator-prey especially at low prey densities.

Obtained results showed that handling time was significantly lower on sweet pepper than cucumber. Therefore, predator spent less time for handling and subduing the prey on the smooth sweet pepper leaves to have access to

prey. Generally, three factors affect the handling time of natural enemies including time spent pursuing and capturing prey, time spent for eating a prey and time spent digesting a prey (Hassell, 1978). Thus, a possible explanation among other reasons for higher handling time of predator on cucumber leaves might be that cucumber leaf trichomes impede the movement of legless predator larvae subsequently interfere its searching efficiency. Moreover, it has been hypothesized that leaf trichomes may provide shelter for prey, making them less vulnerable against their predators (Sabelis and van Rijn, 1997). Thus cucumber leaf trichomes and domatia may provide shelter for small cotton aphid nymphs and cause predator spend more time pursuing and capturing prey. In addition, it seems that secreted honeydew of *A. gossypii* on hairy leaf cucumber tangled more severely than sweet pepper smooth leaf, again slowing predator movement.

Based on the results, this predator showed high maximum predation rate on two host plants theoretically. Although killing 11.75 nymphs in one hour seems considerable for a predator larvae, but this predator has a specific predation behavior in such a way that except some first prey items, it eats next preys partially (personal observations). This phenomenon incurs higher mortality, so killing 11.75 aphid nymphs per hour seems to be possible.

The voracity of *E. balteatus* decreased after peaking at densities of 250 and 350 aphid nymphs on cucumber and sweet pepper respectively. Several reasons may be considered including reaching to satiation level of predator. Additionally, experimental arena saturates at those densities that it may cause unwillingness of predator to continue feeding.

At the high aphid densities, abundant honeydew secretions appeared to repel predators so stimulating them to stop feeding and leave the arena. Another issue is that except density of 64 aphid nymphs, at other prey densities, prey consumption of *E. balteatus* on sweet pepper was significantly higher than on cucumber. Some other researchers have addressed the voracity of *E.*

balteatus in the laboratory. Hong and Hung (2010) reported that predation capacity of third instar larvae of *E. balteatus* on *A. gossypii* was 17.9 ± 0.28 and 17.2 ± 0.54 prey per day at 27.5°C and 30.6°C respectively. Totally, this predator during pre adult period kills 32.2 ± 0.62 and 30.6 ± 1.04 *A. gossypii* per day at 27.5°C and 30.6°C respectively. They showed the feeding capacity of the *E. balteatus* larvae on *A. gossypii* was similar with that on *M. persicae* (31.2 and 31.4 prey per day, respectively) and significantly greater than that on *A. craccivora* (28.2 prey per day).

Our results address the dearth of information about host plant-syrphid interactions, which have not been studied extensively (Verheggen et al., 2009). Obtained information in this study may be useful for the evaluation of *E. balteatus* as a candidate for the biological control of aphids especially on smooth surfaced plant leaves. Results indicate that host plant traits influence the ability of *E. balteatus* to respond to prey density changes and suggest that this predator is able to show a good activity on the relatively smooth surfaces of plants. Furthermore, it has been shown that hairy plant surfaces negatively affect the host plant acceptance as oviposition site for *E. balteatus* females (Almohammad et al., 2009) that it may be due to unsuitability of host plants as habitat for predatory larvae. This research again emphasized that in evaluation of one candidate natural enemy, the tritrophic relationship should be taken into consideration.

Functional response experiments can provide a relatively rapid way to estimate the effects of plant morphology and chemistry on the efficiency of a natural enemy that is searching for prey (Messina and Hanks, 1998). Nevertheless, in interpreting and generalizing their results to natural conditions should be cautious. Moreover, definition of functional responses in the laboratory using simple environments and a single prey type may be of limited value to forecast predator behavior under field conditions. In the field, arthropod predators are faced with complex environments and multiple prey conditions (Hoddle, 2003).

Therefore, it would be necessary to measure functional response of predators in a more real condition and results suggest the need for additional work to confirm whether effects would be representative of field conditions.

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اثر گیاه میزبان بر واکنش تابعی و نرخ مصرف *Episyrphus balteatus* (Diptera: Syrphidae)

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چکیده: واکنش تابعی یکی از مهم‌ترین برهمکنش‌های شکارگر- شکار است که نوع و پارامترهای آن می‌تواند تحت تأثیر عوامل مختلفی از جمله ویژگی‌های گیاه میزبان قرار گیرد. در این تحقیق اثر سطح برگ‌های خیار و فلفل روی واکنش تابعی و نرخ مصرف شکار لارو سن سوم مگس *Episyrphus* برگ‌های خیار و فلفل روی واکنش تابعی و نرخ مصرف شکار لارو سن سوم مگس *Episyrphus* (*Episyrphus balteatus* (De Geer, 1776) (Diptera: Syrphidae) نسبت به پوره‌های سن سوم شته جالیز *Aphis gossypii* Glover (Hemiptera: Aphididae) مورد بررسی قرار گرفت. پرورش شکارگر و آزمایش‌های واکنش تابعی در شرایط آزمایشگاهی (دمای 1 ± 22 درجه سلسیوس، رطوبت نسبی 10 ± 60 درصد و دوره نوری ۱۶:۸ تاریکی: روشنایی) انجام گرفت. نتایج نشان داد که سطح برگ گیاهان میزبان، تراکم-های مختلف شکار و برهمکنش آن‌ها دارای اثر معنی‌داری روی تعداد طعمه خورده شده هستند. رگرسیون لوجیستیک نشان‌دهنده واکنش تابعی نوع سوم روی برگ‌های هر دو گیاه میزبان بود. مقادیر ثابت b و زمان دستیابی به ترتیب روی برگ‌های خیار و فلفل به ترتیب 0.00231 و 0.00351 بر ساعت و همچنین 0.14 ساعت و 0.095 ساعت بود. به علاوه، سطح برگ گیاهان و تراکم‌های مختلف شکار دارای اثرات معنی‌داری روی نرخ مصرف شکار و میزان پرخوری شکارگر بودند. بیشینه مقدار پرخوری شکارگر به ترتیب روی برگ‌های خیار و فلفل $7/71 \pm 180/73$ و $11/71 \pm 282/25$ پوره شته جالیز بود. این نتایج بر اهمیت ویژگی‌های فیزیکی سطح برگ گیاهان میزبان روی عملکرد و کارایی جستجوگری دشمنان طبیعی که برای بهینه‌سازی کنترل بیولوژیک باید لحاظ شود تأکید می‌کند.

واژگان کلیدی: ویژگی‌های فیزیکی، تریکوم‌ها، نرخ شکارگری، زمان دستیابی، مگس‌های سیرفید