

Functional response of *Stethorus gilvifrons* (Col.: Coccinellidae) to different densities of *Eutetranychus orientalis* (Acari: Tetranychidae) in laboratory

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Abstract

The stage specific functional response of the acarophagous ladybird beetle *Stethorus gilvifrons* Mulsant to varying densities of citrus brown mite *Eutetranychus orientalis* (Klein) eggs was examined in a simplified castor bean leaf arena under laboratory conditions. All stages of *S. gilvifrons* were individually isolated for 24 hours with different prey densities at 30°C and a photoperiod of 14: 10 (L: D). The number of prey consumed by the predator was checked after 24 hours. Each larval stage of *S. gilvifrons* showed a type II functional response when 88 eggs out of 120 eggs were consumed by the fourth-instar larva. Based on the random predator equation, the estimated attack rates of *S. gilvifrons* were 0.065, 0.089, 0.143, 0.125 and 0.046 per hour while the estimated handling times stood at 0.141, 0.166, 0.150, 0.134 and 0.082 per hour for the first, second, third and fourth instar as well as the adult female respectively. The species *S. gilvifrons* showed to be an effective predator on *E. orientalis* under controlled conditions. The results suggest that the simultaneous use of the both fourth-instar larvae and adult females of the acarophagous ladybird beetle could increase the rate of predation in the field.

Key words: Functional response, *Stethorus gilvifrons*, *Eutetranychus orientalis*, Iran

چکیده

واکنش تابعی سنین مختلف رشدی کفشدوزک کنه‌خوار *Stethorus gilvifrons* Mulsant نسبت به تراکم‌های مختلف تخم کنه‌ی قهوه‌ای مرکبات *Eutetranychus orientalis* (Klein) روی برگ گیاه کرچک در شرایط آزمایشگاهی مورد بررسی قرار گرفت. کلیه‌ی سنین مختلف رشدی *S. gilvifrons* به صورت جداگانه با تراکم‌های مختلف طعمه در دمای ۳۰ درجه‌ی سیلسیوس و دوره‌ی نوری ۱۰: ۱۴ (تاریکی: روشنایی) گذاشته شدند. تعداد طعمه‌های مصرف‌شده به‌وسیله‌ی هر شکارگر بعد از ۲۴ ساعت یادداشت گردید. کلیه‌ی مراحل مختلف رشدی، واکنش تابعی نوع II را نشان دادند و هنگامی که ۱۲۰ تخم کنه فراهم بود لارو سن چهارم کفشدوزک تا ۸۸ تخم را مصرف نمود. بر اساس معادله‌ی شکارگری تصادفی، نرخ حمله‌ی سنین اول، دوم، سوم، چهارم لاروی و کفشدوزک بالغ ماده به‌ترتیب برابر با ۰/۰۶۵، ۰/۰۸۹، ۰/۱۴۳، ۰/۱۲۵ و ۰/۰۴۶ و زمان دستیابی مراحل رشدی فوق به‌ترتیب برابر با ۰/۱۴۱، ۰/۱۶۶، ۰/۱۵۰، ۰/۱۳۴ و ۰/۰۸۲ ساعت بود. گونه‌ی *S. gilvifrons* نشان داد که در شرایط کنترل‌شده می‌تواند شکارگر مؤثری برای کنترل کنه‌ی قهوه‌ای مرکبات باشد و پیشنهاد شد که حضور هم‌زمان لاروهای سن چهارم و بالغین ماده این کفشدوزک می‌تواند کارایی آن را در کاهش جمعیت آفت در مزرعه افزایش دهد.

واژگان کلیدی: واکنش تابعی، *Stethorus gilvifrons*، *Eutetranychus orientalis*، ایران

Introduction

The citrus brown mite *Eutetranychus orientalis* (Klein) is one of the most important pests of the southwestern agricultural systems in Iran, causing significant damage to fruit trees in addition to horticultural and ornamental plants (Jeppson *et al.*, 1975; Modares Awal, 2001; Mossadegh & Kocheili, 2003; Kamali *et al.*, 2004).

Traditionally, *E. orientalis* is being chemically controlled by acaricides which usually results in the problems of pest resistance and contamination of the harvested crops and consumed products. Efforts are therefore being made to develop an integrated control programme of *E. orientalis* using native populations of predatory coccinellid beetles.

Various species of the genus *Stethorus* Weise, commonly known as acarophagous ladybird beetles, are predators of agricultural crop pests and significantly contribute to the control of spider mite pests (Roy *et al.*, 2003; Gotoh *et al.*, 2004). The species *Stethorus gilvifrons* Mulsant is one of the two recorded Iranian *Stethorus* species (Modares Awal, 2001; Mossadegh & Kocheili, 2003) which is found in sugarcane and castor bean fields as well as date palm and apple orchards (Hajizadeh, 1995; Kajbaf Vala, 1999; Modares Awal, 2001; Afshari *et al.*, 2007), where it successfully controls various spider mites (Chazeau, 1985; Obrycki & Kring, 1998).

The performance of a predator depends on several characteristics, including functional response. The functional response describes the relationship between an individual's consumption rate and food density (Solomon, 1949), and is classified into three types by Holling (1959). Arthropods have the types II and III responses, although the type II is observed more frequently. Different types of functional responses may have different effects on the dynamics of prey population (Begon *et al.*, 1996).

Although some bionomic studies on *S. gilvifrons* have been conducted (Aksit *et al.*, 2007; Imani, 2008; Matin, 2008; Taghizadeh *et al.*, 2008a, 2008b) no detailed study has been conducted on its functional response to *E. orientalis*. Therefore, this study is intended to evaluate the impacts of different densities of *E. orientalis* egg on the predation rate of adult females and larval stages of *S. gilvifrons* and also to characterize the functional response of *S. gilvifrons* to different densities of the prey, *i.e.* the shape and the coefficients of attack rate and handling time of the response curves.

Materials and methods

Stock culture of *E. orientalis* and *S. gilvifrons*

The specimens of the prey *E. orientalis* and predator *S. gilvifrons* were collected from the castor bean (*Ricinus communis* L.) leaves at Shahid Chamran University campus, Ahvaz, Iran, in April 2008 and used to start their cultures. The stock colony of *E. orientalis* was maintained on castor bean plants (cv. Ahvazy) grown from seeds and transplanted into soil in plastic pots (20 cm diameter). Infested plants were kept in wooden-framed rearing cage (120

× 60 × 60 cm) covered with nylon mesh of 120 μ aperture. The cages were held in the laboratory conditions at 25°C ± 1°C, 65% ± 5% RH. The photoperiod was 14: 10 (L: D) with illumination (4000 lux) provided from fluorescent lamps. The plants remained in the cages until they were severely damaged by the spider mites and if it was required new plants were included. After several generations, mites from the stock colony were used for conducting the experiments.

The predator *S. gilvifrons* stock culture was preserved in a separate laboratory and the rearing cages were provided with all developmental stages of the prey *E. orientalis* as the food source on castor plants. Once a week, new *E. orientalis*-infested castor plants were added to the cages. The conditions of the laboratories were identical. The experiments were conducted at Department of Plant Protection, Shahid Chamran University, Ahvaz, Iran.

The identities of *E. orientalis* and *S. gilvifrons* were confirmed by Drs K. Kamali and H. Hodek, respectively and voucher specimens were deposited in the insect collection of Shahid Chamran University.

Functional response

The experimental arena consisted of a castor bean leaf ($\approx 16 \text{ cm}^2$), floating dorsal side up on a water-soaked polyurethane pad in a 8.5cm-diameter Petri dish. The prey densities were 4, 8, 12, 24, 48, 96 and 120 eggs (< 24 h old) of *E. orientalis*. After 24 hours the number of prey eggs eaten was determined by counting the remaining intact eggs. In this study, we focused mainly on prey eggs consumed by different developmental stages of *S. gilvifrons*, because the egg stage comprises the major proportion of an *E. orientalis* population (Imani, 2008). Different predator stages, the first, second, third and fourth-instar larvae in addition to adult females (< 24 h old), of *S. gilvifrons* were individually transferred with a fine paintbrush onto the leaf discs. The dishes were lidded and ventilated with a 120 μ mesh. At least five replications of each prey density were set up simultaneously. The experiments were performed in a growth chamber at 30°C ± 1°C, 60% ± 5% RH and 14: 10 (L: D). The observations were made possible by a stereomicroscope.

Data analysis

The analysis of variance was used to test differences in the daily prey consumption at various prey densities in relation to predator developmental stages using PROC GLM in SAS

(SAS Institute, 2001). The Fisher's protected LSD test was used for mean separation ($P < 0.05$) (SAS Institute, 2001).

We followed the methods of Juliano (2001) to fit the data to Rogers' (1972) random predator equation. Using this method, the type of functional responses (I, II or III) displayed by the data is first determined by linear regression in PROC CATMOD (SAS Institute, 2001). In this method, the polynomial function that describes the relationship between the proportion of eggs eaten at each density and each initial density is determined. The negative first term in the function is an indication of a Type II functional response while the positive first term displays a Type III functional response (Juliano, 2001). Juliano's equation:

$$N_a/N_0 = \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3) / (1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3))$$

Where N_a is the number of prey being consumed by the predator, N_0 is the initial number of prey, and P_0 , P_1 , P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficient, respectively, estimated using the method of maximum likelihood (Juliano, 2001).

After determining the type of functional response, the data were fit to the random predation equation in PROC NLIN (SAS Institute, 2001). Instantaneous search rate (a) and handling time (T_h) were estimated by fitting Rogers' equation:

$$N_a = N_t [1 - \exp(-a(T_h N_t - T))]$$

Where N_a is the number of prey being eaten by the predator, N_t is the initial density of prey, T stands for the time available for searching during the experiment, " a " is the instantaneous attack rate, P_1 is the number of predators and T_h is the amount of time the predator handles each prey.

Results

Predation ability

The number of eggs of *E. orientalis* consumed by each developmental stage increased significantly as their densities increased (table 1). The first and second-instar larvae consumed least amount of eggs. The fourth-instar larvae consumed most, followed by third-instar larvae and adult females. Predation rate was not significantly different among developmental stages, except for prey densities of 12, 96 and 120 eggs (table 1).

Functional response

Parameter estimates from the polynomial model of proportion of *E. orientalis* eggs consumed by *S. gilvifrons* over a 24-hour period versus *E. orientalis* eggs are presented in the table 2. Estimates of the linear parameter (P_1) were significantly negative. The functional response data for *S. gilvifrons* preying on *E. orientalis* eggs over a 24-h period exhibited a Type II response for all developmental stages (fig. 1). Predation efficiency increased as *S. gilvifrons* developed from one developmental stage to another. The parameters of attack rate (a) and handling time (T_h) show this relationship numerically (table 3). The attack rate was highest in the third and fourth-instar larvae, followed by the second-instar larvae. Handling times for the fourth-instar larvae and adult females were 0.134 h and 0.082 h, respectively, being shorter than the handling times of other stages.

Table 1. Voracity (number of prey eaten \pm SE) of *S. gilvifrons* 1st, 2nd, 3rd, 4th instar larvae and adult females fed on different densities (number of prey provided) of *E. orientalis* egg.

Prey density	Voracity \pm SE				Adult female
	1 st instar	2 nd instar	3 rd instar	4 th instar	
4	4.0 \pm 0.00a	3.6 \pm 0.24a	3.6 \pm 0.24a	3.6 \pm 0.24a	4.0 \pm 0.00a
8	5.6 \pm 0.24a	5.8 \pm 0.37ab	6.0 \pm 0.31a	5.6 \pm 0.24c	7.4 \pm 0.24ab
12	8.0 \pm 0.45a	8.4 \pm 0.24c	8.8 \pm 0.37a	9.2 \pm 0.97c	11.4 \pm 0.24c*
24	18.0 \pm 1.00b	19.4 \pm 0.93d	18.8 \pm 0.91b	20.4 \pm 0.51d	23.6 \pm 0.24d
48	30.2 \pm 2.27c	35.4 \pm 2.20e	40.0 \pm 1.92c	37.8 \pm 1.53e	46.0 \pm 0.84e
96	59.0 \pm 3.16d	72.2 \pm 2.31f	85.0 \pm 1.41d	86.6 \pm 1.63f*	83.2 \pm 2.89f
120	61.2 \pm 3.12f	74.6 \pm 2.20f	87.6 \pm 2.2d	88.4 \pm 1.30f*	85.0 \pm 2.71f

Means within a column followed by different letters and means within a row followed by an asterisk (*) are significantly different at $P < 0.05$ (LSD test).

Table 2. Maximum likelihood estimates (SE) for parameters of the polynomial model fit to proportion of prey consumed versus initial prey density.

Parameter	Larvae				Female adult
	First-instar	Second-instar	Third-instar	Fourth-instar	
P_0	0.418 (0.3246)	1.4062 (0.3397)	1.469 (0.3536)	1.621 (0.3443)	5.128 (0.7951)
P_1	-0.0385 (0.0194)	-0.0234 (0.0203)	-0.0328 (0.023)	-0.0468 (0.0225)	-0.183 (0.0415)
P_2	0.00059 (0.00031)	0.00054 (0.00034)	0.001 (0.00039)	0.0013 (0.00038)	0.00328 (0.00063)
P_3	-3.15 (1.486)	-3.44 (1.621)	-7.09 (1.91)	-8.18 (1.92)	2.918 (0.0002)

Discussion

Hodek & Honek (1996) reported that the fourth-instar larvae of the coccinellid beetles are generally responsible for approximately 60% - 80% of total prey consumption at the larval stage. Being observed in our study, the fourth-instar larvae were more voracious than adult females, as reported in previous studies by Lee & Kang (2004), Cabral *et al.* (2006) and Moura *et al.* (2006) for aphidophagous ladybirds. The higher voracity of the fourth-instar larvae is possibly due to high requirements of energy intake for their growth and their critical weight attainment for the pupal stage (Hodek & Honek, 1996).

Table 3. Attack rate (a) and handling time (T_h) estimated by Rogers' equation and respective standard error (SE), and 95% confidence intervals, for the 1st, 2nd, 3rd, 4th instar larvae and adult females of *S. gilvifrons* fed on *E. orientalis* eggs.

Life stage	Parameters	Estimates	Asymptote (SE)	95% CI		T/ T_h	R ²
				Lower	Upper		
1 st instar	a	0.065	0.010	0.0435	0.0875	116.0	0.98
	T_h	0.207	0.036	0.1338	0.2820		
2 nd instar	a	0.089	0.014	0.0588	0.1194	144.6	0.99
	T_h	0.166	0.029	0.1051	0.2267		
3 rd instar	a	0.143	0.033	0.0796	0.2115	160.0	0.97
	T_h	0.150	0.029	0.1001	0.2204		
4 th instar	a	0.125	0.028	0.0664	0.1797	179.1	0.99
	T_h	0.134	0.034	0.0644	0.2014		
Adult females	a	0.046	0.004	0.0372	0.0552	292.7	0.97
	T_h	0.082	0.020	0.0372	0.1224		

Stethorus gilvifrons exhibited Type II functional response at all developmental stages against *E. orientalis*. The Type II functional response curve of *S. gilvifrons* has also been reported by Afshari (1998) on *Oligonychus sacchari* (McGregor), by Mehrkhou (2009) on *Tetranychus urticae* Koch and by Matin (2008) on *Oligonychus afasiaticus* McGregor. However, Sohrabi & Shishehbor (2007) reported the Type III functional response for the adults of *S. gilvifrons* feeding on *Tetranychus turkestanii* Ugarov & Nikolski.

The low predation rates observed in the first and second-instar larvae of *S. gilvifrons* can be probably due to their low attack rates and longer prey handling times (table 3). The small size and slow movement of the first and second-instar larvae could be the reasons for the low predation rates of these stages. Though the third-instar larvae showed the highest attack rate, their maximum mean egg consumption was much less than fourth-instar larvae and adult females, probably because of their longer handling time (table 3). Moreover, the highest prey

consumption, relatively high attack rate and short handling time of fourth-instar larvae of *S. gilvifrons* is an indication of their striking voracity comparing to other stages.

The estimated values of attack rate and handling time obtained in the present study fall within the published range of "a" and T_h for *S. gilvifrons* feeding on different tetranychid prey species (table 4).

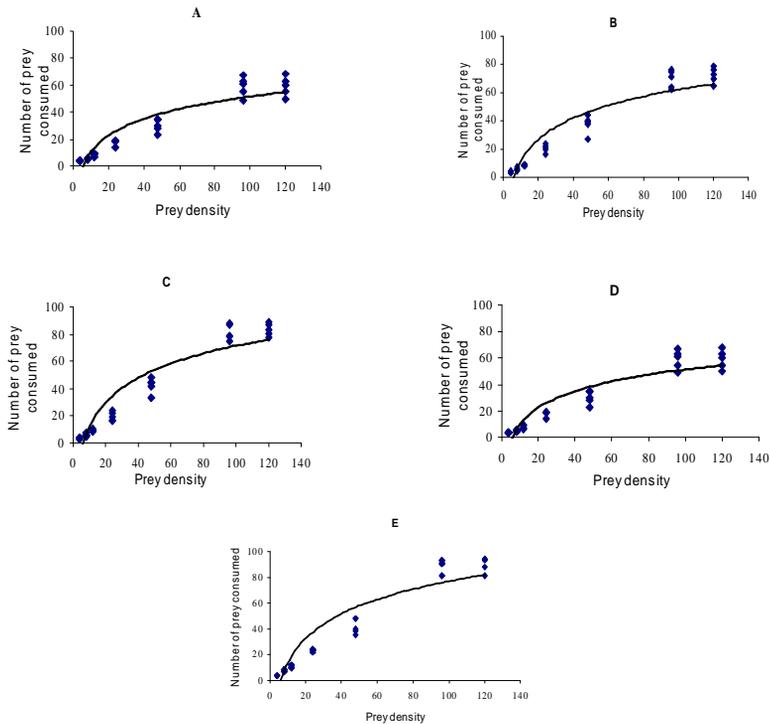


Figure 1. Functional responses of different instar larvae and adult females of *S. gilvifrons* to *E. orientalis* eggs on castor bean leaf over a 24-hour period. (A) 1st instar, (B) 2nd instar, (C) 3rd instar, (D) 4th instar, (E) adult females. Each data point represents the observed number of eggs consumed by *E. orientalis*. Curve was fitted using the random predator equation.

A variety of responses had been reported on different coccinellid species, i.e. higher handling time (T_h) and attack rate (a) for fourth-instar larvae than adults in *Hippodamia*

convergens Guerin-Meneville (Wells & McPherson, 1999), higher handling time and lower attack rate for fourth-instar larvae than adults of *Coleomegilla maculata* DeGeer (Munyaneza & Obrycki, 1997), lower handling time and higher attack rate for fourth-instar larvae than adults of *Harmonia axyridis* (Pallas) and *Scymnus creperus* Mulsant (Wells *et al.*, 2001; Lee & Kang, 2004). Our results indicates higher handling time and attack rate for fourth-instar larvae than adult females.

O'Neil (1989) and Wiedenmann & O'Neil (1991) criticized the functional response experiments carried out in small laboratory arenas. They stated that in the field, various factors, including large searching areas, host plants and weather conditions can influence the effectiveness of predators. Furthermore, predators are rarely found in nature as single individuals. The simultaneous presence of different developmental stages of a prey as well as occurrence of various prey species on a leaf or plant can affect the functional responses of predators. Thus it is of interest to know how the response of predators will be in nature where the system tends to be more complex.

Table 4. Attack rate (a) and handling time (T_h) estimated for *S. gilvifrons* fed on different mite species.

Mite Prey	a	T_h	T/T_h	Reference
<i>Tetranychus urticae</i>	0.041	0.233	103.00	Mehrkhou, 2009
<i>Olygonychus afasiaticus</i>	0.085	0.138	173.16	Matin, 2008
<i>Tetranychus turkestanii</i>	0.0012	0.415	57.82	Sohrabi & Shishebor, 2007

The results of the current study have improved our understanding of the *S. gilvifrons*-*E. orientalis* interactions under laboratory conditions. The findings will be also useful for the development of a viable strategy for the biological control of *E. orientalis* by *S. gilvifrons*. Our results prove that the simultaneous use of both fourth-instar larvae and adult females of *S. gilvifrons* could have synergetic effects on the suppression of the pest in the field and increase the success of the biocontrol program. It is to be noted that the early season release of the sexually mature adults of *S. gilvifrons* in the field could heighten the efficiency of the program as the ladybirds mostly lay their eggs over a relatively short period of time just early before peak prey infestation (Hemptinne *et al.*, 2000). This strategy will better support the survival of the offspring of the ladybirds because they would be able to oviposit in the prey patches. Consequently, at the time that mite colonies reach their peaks, there will be high populations of fourth-instar larvae of *S. gilvifrons* within the field engaged in intensive search activities for the suppression of prey patches.

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References

- Afshari, G. A.** (1998) A survey on the ladybirds belong to genus *Stethorus* and study on the biology, prey consumption and population dynamics of *Stethorus gilvifrons* in sugarcane farms in Khuzestan, Iran. M. Sc. Thesis. Shahid Chamran University, Ahvaz, Iran. 158 pp.
- Afshari, A., Mossadegh, M. S. & Kamali, K.** (2007) Seasonal changes and spatial distribution of sugarcane mite, *Oligonychus sacchari* (Prostigmata: Tetranychidae) and predatory ladybird, *Stethorus gilvifrons* (Mulsant) (Coleoptera: Coccinellidae) in sugarcane fields of Ahvaz. *Scientific Journal of Agriculture* 30, 135-147.
- Aksit, T., Cakmak, I. & Ozer, G.** (2007) Effect of temperature and photoperiod on development and fecundity of an acarophagous ladybird beetle, *Stethorus gilvifrons*. *Phytoparasitica* 35, 357-366.
- Begon, M., Mortimer, M. & Thompson, D. J.** (1996) *Population ecology*. 3rd ed. 680 pp. Blackwell Science, Oxford.
- Cabral, S. G. M., Soares, A. O., Moura, R. & Garcia, P.** (2006) Suitability of *Aphis fabae*, *Myzus persicae* (Homoptera: Aphididae) and *Aleyrodes proletella* (Homoptera: Aleyrodidae) as prey for *Coccinella undecimpunctata* (Coleoptera: Coccinellidae). *Biological control* 39, 434-440.
- Chazeau, J.** (1985) Predaceous insects. pp. 211-246 in Helle, W. & Sabelis, M. W. (Eds) *World crop pests; spider mites: their biology, natural enemies and control*. 550 pp. Elsevier Publication.
- Gotoh, T. M., Nozawa, H. S. & Yamaguchi, K.** (2004) Prey consumption and functional response of three acarophagous species to eggs of the two-spotted spider mite in the laboratory. *Applied Entomology and Zoology* 39, 97-105.
- Hajizadeh, J.** (1995) Identification of *Stethorus* coccinellid beetles in Tehran province and study on biology, and possibility of production of *Stethorus gilvifrons* Mulsant. Ph. D. Thesis. Tarbiat Modares University, Tehran, Iran. 198 pp.

- Hemptinne, J. L., Doumbia, M. & Dixon, A. F. G.** (2000) Assessment of patch quality by ladybirds: role of aphid and plant phenology. *Journal of Insect Behavior* 13(3), 353-359.
- Hodek, I. & Honek, A.** (1996) *Ecology of Coccinellidae*. 464 pp. Kluwer Academic Publishers.
- Holling, C. S.** (1959) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91, 385-398.
- Imani, Z.** (2008) Biology and predation of *Stethorus gilvifrons* Mulsant on oriental red mite, *Eutetranychus orientalis* Klein. M. Sc. Thesis. Shahid Chamran University, Ahvaz, Iran. 150 pp.
- Jeppson, L. R., Keifer, H. H. & Baker E. W.** (1975) *Mites injurious to economic plants*. 613 pp. University of California Press.
- Juliano, S. A.** (2001) Nonlinear curve fitting: predation and functional response curves. pp. 178-196 in Scheiner, S. M. & Gurevitch J. (Eds) *Design and analysis of ecological experiments*. 782 pp. Oxford University Press.
- Kajbaf Vala, R.** (1999) Investigation on the biology and production of *Stethorus gilvifrons* Mulsant for biological control of date palm spider mite, *Olygonychus afrasiaticus* McGregor in Khuzestan. Final Report. Agricultural Research Center, Ahvaz, Iran. 35 pp.
- Kamali, K., Ostovan, H. & Atamehr, A.** (2004) *A catalog of mites and ticks (Acari) of Iran*. 192 pp. Islamic Azad University Scientific Publication Center.
- Lee, J. H. & Kang, T. J.** (2004) Functional response of *Harmonia oxymidis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biological Control* 31, 306-310.
- Matin, M.** (2008) Biology and predation of *Stethorus gilvifrons* Mulsant fed on date dust mite, *Olygonychus afrasiaticus* McGregor. M. Sc. Thesis. Mohaghegh Ardebili University, Ardebil, Iran. 73 pp.
- Mehrkhou, F.** (2009) Foraging behavior of *Stethorus gilvifrons* (Coleoptera: Coccinellidae) on *Tetranychus urticae* (Acari: Tetranychidae). M. Sc. Thesis. Tarbiat Modares University, Tehran, Iran. 81 pp.
- Modares Awal, M.** (2001) *List of agricultural pests and their natural enemies in Iran*. 429 pp. Ferdowsi University Press.

- Mossadegh, M. S. & Kocheili, F.** (2003) *A semi descriptive checklist of identified species of arthropods (agricultural, medical, ...) and other pests from Khuzestan, Iran*. 574 pp. Shahid Chamran University Press.
- Moura, R., Garcia, P., Cabral, S. & Soares, A. O.** (2006) Does primicarb affect the voracity of the euriphagous predator, *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae)? *Biological control* 38, 363-368.
- Munyanza, J. & Obrycki, J. J.** (1997) Functional response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle eggs (Coleoptera; Chrysomelidae). *Biological control* 8, 215-224.
- Obrycki, J. J. & Kring, T. J.** (1998) Predacious Coccinellidae in biological control. *Annual Review of Entomology* 43, 295-321.
- O'Neil, R. J.** (1989) Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). *Journal of Kansas Entomological Society* 62, 148-155.
- Rogers, D.** (1972) Random search and insect population models. *Journal of Animal Ecology* 41, 369-383.
- Roy, M., Brodeur, J. & Clutier, C.** (2003) Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey. *BioControl* 48, 57-72.
- SAS Institute**, (2001) *SAS user's guide: statistics, version 8.2*. 6th ed. SAS Institute, Cary, NC.
- Sohrabi, F. & Shishehbor, P.** (2007) Functional and numerical response of *Stethorus gilvifrons* feeding on *Tetranychus turkestani*. *Pakistan Journal of Biological Sciences* 10, 4563-4566.
- Solomon, M. E.** (1949) The natural control of animal populations. *Journal of Animal Ecology* 18, 1-35.
- Taghizadeh, R., Fathipour, Y. & Kamali, K.** (2008a) Temperature-dependent development of acarophagous ladybird, *Stethorus gilvifrons* (Mulsant) (Coleoptera: Coccinellidae). *Journal of Asia-Pacific Entomology* 11, 145-148.
- Taghizadeh, R., Fathipour, Y. & Kamali, K.** (2008b) Influence of temperature on life-table parameters of *Stethorus gilvifrons* Mulsant (Coleoptera: Coccinellidae) fed on *Tetranychus urticae* Koch. *Journal of Applied Entomology* 132, 638-645.

- Wiedenmann, R. N. & O'Neil, R. J.** (1991) Laboratory measurement of the functional response of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). *Environmental Entomology* 20, 610-614.
- Wells, M. L. & McPherson, R. M.** (1999) Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). *Environmental Entomology* 28(4) 768-773.
- Wells, M. L., McPherson, R. M., Ruberson, J. R. & Herzog, G. A.** (2001) Coccinellids in cotton: population response to pesticide application and feeding response to cotton aphids (Homoptera: Aphididae). *Environmental Entomology* 30(4) 785-793.

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