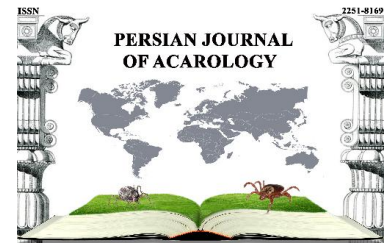




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## Article

### Daily consumption and functional response of *Stethorus gilvifrons* (Coleoptera: Coccinellidae) and *Orius albidipennis* (Hemiptera: Anthocoridae) to *Tetranychus urticae* (Acari: Tetranychidae)

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#### ABSTRACT

The two-spotted spider mite, *Tetranychus urticae* Koch, is one of the most economically important pests on a wide range of crops around the world. Consumption rate and functional responses of all larval stages, male and female of *Stethorus gilvifrons* (Mulsant) and *Orius albidipennis* (Rueter) to the varying densities of eggs, protonymphs and females of *T. urticae* were evaluated under laboratory conditions ( $27 \pm 1$  °C,  $65 \pm 5\%$  RH and 16L/8D h photoperiod). Functional response type was determined by a logistic regression model. The Rogers model was used to estimate attack rate ( $a$ ) and handling time ( $T_h$ ). The results indicated that the functional responses of different stages of two predators were type III on *T. urticae* eggs and type II on *T. urticae* protonymphs and females. The shortest handling time ( $T_h$ ) of both predators were observed on eggs followed by protonymphs and females of *T. urticae*. The highest and the lowest attack rate ( $a$ ) were observed by the male and first instar larva in *S. gilvifrons* and female and first instar nymph in *O. albidipennis* respectively. The maximum daily attack rates ( $T/T_h$ ) were 153.5, 114.4 and 76.07 for *S. gilvifrons*, and 134.1, 91 and 55.3 for *O. albidipennis* by feeding on egg, protonymph and female *T. urticae* respectively. The handling time ( $T_h$ ) of *S. gilvifrons* adults were shorter than that of *O. albidipennis*. The results suggested that both predators exhibited suitable efficacy on all stages of *T. urticae*, however *S. gilvifrons* acted more effectively than the other predator in laboratory conditions considering higher consumption rate, shorter handling time and higher attack rate.

**KEY WORDS:** Biological control; consumption rate; functional response; predator; two-spotted spider mite.

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## INTRODUCTION

Two-spotted spider mite, *Tetranychus urticae* Koch is an important pest mite in various agricultural crops around the world (Jeppson *et al.* 1975; Takafuji *et al.* 2000; Zhang 2003; Song *et al.* 2016). This mite is a serious pest of over 200 economically important crops (Helle and Sabelis 1985). *Tetranychus urticae* has become a serious problem due to large scale use of chemical insecticides (Uddin *et al.* 2017). Widespread acaricide usage has eliminated many natural enemies of the spider mites, resulting in the reduction of a predation pressure on the mite (Wu *et al.* 2016). In recent years, several strategies have been developed to control *T. urticae* on economically important

crops (Bostanian *et al.* 2003). One of these strategies is using predatory mites and insects in integrated pest management (IPM) programs (Roy *et al.* 2005).

All known species of the genus *Stethorus* are predators of spider mites, and several species have been used as biocontrol agents of tetranychid mites in agricultural systems (Roy *et al.* 1999). The predatory ladybird beetle, *Stethorus gilvifrons* (Mulsant) is a specialist predator preying on different life stages of two-spotted spider mite. However, there are only few works specifically dealing with either the voracity and/or the feeding behavior of this predator (Hajizadeh *et al.* 1992; Afshari *et al.* 2001; Kheradpir *et al.* 2006). *Stethorus gilvifrons* has dispersed in the Middle East and Southern Europe (Akist *et al.* 2007; Biddinger *et al.* 2009; Mofleh *et al.* 2014). Considering its acceptable searching ability and high consumption rate, this predator can be considered as a good candidate for augmentative release program in pest hot spots both in outdoor fields and greenhouses (Ahmed and Ahmed 1989).

*Orius albidipennis* (Reuter) is a biological control agent of particular interest, which is frequently found in large numbers in various agricultural habitats (Chyzik *et al.* 1995; Cocuzza *et al.* 1997). It is widely distributed in the Mediterranean basin and the Atlantic zone of western Europe (Péricart 1972). In Iran, this predator is widely distributed and reported from different provinces (Ghahari *et al.* 2012; Modarres Awal 2012). Numerous studies have been conducted to evaluate prey-preference, efficacy and predation rate of *Orius albidipennis* on different pests in Iran (Hosseinyinia and Malkeshy 2003; Kosari and Kharazi-Pakdel 2006; Madadi *et al.* 2009). Mirhelli (2000) studied the mass rearing methods and biology of this predator in laboratory conditions. Chyzik *et al.* (1995) reported this species as one of the most abundant predators attacking *Frankliniella occidentalis* (Pergande) in the Canary Islands. Because of a high heat tolerance and lack of photoperiod-induced diapause, this species could be an ideal candidate for mass rearing and augmentative releases in subtropical and tropical areas (Sobhy *et al.* 2010).

One of the most important methods to assess the efficacy of natural enemies in regulating the pest populations is the study of their foraging behavior characteristics such as functional response (Houck and Strauss 1985). The functional response has been used extensively in population ecology and foraging theory to study the potential of predators to regulate pest populations (Murdoch and Oaten 1975). Functional response measures the predation rate as a function of prey density allowing estimation of the attack rate and handling time of the biocontrol agent (Britto *et al.* 2009). To further understand the comparative consumption rate and predatory abilities of *S. gilvifrons* and *O. albidipennis* against the different stages of *T. urticae*, and to compare the potential of these two predators in varying densities of *T. urticae*, we evaluated functional responses of different stages of these two predators against *T. urticae* eggs, protonymphs and females. This study can help us to compare potential efficacy of a specialist predator with a generalist one in a situation where major pest is the two spotted spider mite and no other alternative is available.

## MATERIALS AND METHODS

### Cultures

**a) Two spotted spider mite** – The two spotted spider mite was originally collected from infested corn plants (*Zea mays* L.) in Moghan region (39.65° N, 47.91° E), Ardabil province, Iran and reared on bean plants (*Phaseolus vulgaris* Linnaeus var. Khomain) in a glasshouse of Faculty of Agriculture, University of Tabriz, Iran. The bean seeds were sown in plastic pots (25 cm in diameter) containing field soil within a wooden-framed cage (100 × 100 × 60 cm) covered by nylon mesh at 25 ± 1 °C, 70 ± 5% RH and 14L/10D h photoperiod.

**b) Predators** – The individuals of *Orius albidipennis* and *Stethorus gilvifrons* were collected from corn and soybean fields in the same location in summer 2015 and 2016. They were reared in a

growth chamber (Iran Khodsaz, IKH, RH) at  $27 \pm 1$  °C,  $65 \pm 5\%$  RH and 16L/8D h photoperiod (see mass rearing subsections).

**Mass rearing of *Stethorus gilvifrons*** – *Stethorus gilvifrons* were kept for a few generations in plastic boxes of  $20 \times 10 \times 5$  cm covered by muslin at top and filter paper at the bottom. Detached bean leaf infested by the spider mite, *T. urticae*, were used as a food source.

**Mass rearing of *Orius albidipennis*** – This predatory bug (40 per jar) was reared in plastic jars (10 cm diameter  $\times$  20 cm height), covered by muslin using a rubber band. The flour moth, *Ephestia kuehniella* Zeller eggs plus corn pollen were daily supplied. A green bean pod was provided in each jar as an oviposition substrate as well as moisture source. Bean pods with newly deposited eggs were removed and replaced daily. Crumpled tissue papers were included to decrease the contact between individuals and avoid cannibalism.

#### Functional response

The experimental unit consisted of a plastic petri dish (6 cm in diameter, 3 cm height) with a ventilation hole (3 cm in diameter) in the lid covered by a fine nylon gauze. A bullet of cotton was soaked and then spread at bottom of the container and a kidney bean (*Phaseolus vulgaris* L.) detached leaf ( $3 \times 3$  cm) was placed on it upside down. The experiments were conducted in a laboratory at  $27 \pm 1$  °C,  $65 \pm 5\%$  RH and 16L/8D h photoperiod. Different densities of eggs, protonymphs and females of *T. urticae* were offered separately to all larval stages, male and female of *S. gilvifrons* and *O. albidipennis*. The tested densities of eggs and protonymphs of *T. urticae* were 2, 4, 8, 16, 32, 48, 64, 80, 96, 148, 164 and 196 per unit; the same densities except those of above 80 were also used for female *T. urticae*. In order to avoid reproduction of ovipositing females, new females were transferred directly from the stock culture to the experimental arena; also laid prey eggs were removed from the arena in intervals of 7–8 h. Before beginning the experiment, the predators were starved for 24 h. In order to prevent escaping of individual mites and predators, leaf discs were surrounded with strips of filter paper. The total time of the experiment was 24 h. Each treatment had 10 replications. The number of prey eaten was determined by counting intact eggs and the carcasses of protonymphs and adults at the end of the experiment.

#### Data Analysis

The data were analyzed in two steps (Juliano 2001). First, the type of response was determined using a logistic regression of the proportion of prey consumed ( $N_a/N_0$ ) as a function of initial density ( $N_0$ ):

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

where  $N_a$  is the number of prey consumed,  $N_0$  is the initial prey density, ( $N_a/N_0$ ) is the proportion of prey consumed, and  $P_0$ ,  $P_1$ ,  $P_2$  and  $P_3$  are maximum likelihood estimates of the intercept, linear, quadratic and cubic coefficients, respectively. The sign of  $P_1$  and  $P_2$  was used to distinguish the shape of the curves. When the sign of  $P_1$  is negative, the predator displays a Type II functional response indicating that the proportion of prey consumed declines monotonically with the initial number of prey. Otherwise when a positive density-dependent relation of the proportion of consumed prey ( $P_1 > 0$  and  $P_2 < 0$ ) is obtained, the predator displays a Type III functional response (Juliano 2001). In the next step, the handling time and attack rate coefficients of a type II response were estimated using the random predator equation (Royama 1971; Rogers 1972).

**Table 1.** Maximum likelihood estimates ( $\pm$  SE) of the logistic regression parameters representing proportion of different stages of *Tetranychus urticae* consumed by different stages of *Stethorus gilvifrons* as a function of initial prey density.

Predator stages	Parameters	Egg				Protonymph				Female			
		Estimates	$\chi^2$	P		Estimates	$\chi^2$	P		Estimates	$\chi^2$	P	
Larva I	$P_0$	-1.4023 $\pm$ 0.2315	36.70	< 0.0001	0.9429 $\pm$ 0.3306	8.13	0.0043		0.7156 $\pm$ 0.4332	2.73	0.0985		
	$P_1$	0.0369 $\pm$ 0.0133	7.68	0.0056	-0.2092 $\pm$ 0.0447	21.95	< 0.0001		-0.2918 $\pm$ 0.0822	12.60	0.0004		
	$P_2$	-0.0006 $\pm$ 0.0002	13.02	0.0003	0.0046 $\pm$ 0.0015	9.62	0.0019		0.0087 $\pm$ 0.0038	5.39	0.0203		
	$P_3$	-	-	-	-0.00003 $\pm$ 0.00001	6.16	0.0131		-0.00009 $\pm$ 0.00005	3.34	0.0676		
Larva II	$P_0$	-0.4404 $\pm$ 0.2978	2.19	0.1391	1.4510 $\pm$ 0.3346	18.80	< 0.0001		1.6609 $\pm$ 0.4419	14.13	0.0002		
	$P_1$	0.1340 $\pm$ 0.0355	14.26	0.0002	-0.1365 $\pm$ 0.0403	11.49	0.0007		-0.1664 $\pm$ 0.0702	5.63	0.0177		
	$P_2$	-0.0047 $\pm$ 0.0011	17.77	< 0.0001	0.0021 $\pm$ 0.0013	2.63	0.1050		0.0029 $\pm$ 0.0030	0.92	0.3367		
	$P_3$	0.00004 $\pm$ 0.00001	16.43	< 0.0001	-0.00001 $\pm$ 0.00001	0.92	0.3365		-0.00002 $\pm$ 0.00004	0.23	0.6352		
Larva III	$P_0$	0.5526 $\pm$ 0.3201	2.98	0.0843	2.0432 $\pm$ 0.3769	29.39	< 0.0001		2.2402 $\pm$ 0.3885	33.25	< 0.0001		
	$P_1$	0.0776 $\pm$ 0.0378	4.21	0.0401	-0.1007 $\pm$ 0.0412	5.98	0.0145		-0.1275 $\pm$ 0.0426	8.98	0.0027		
	$P_2$	-0.0029 $\pm$ 0.0012	5.88	0.0153	0.0012 $\pm$ 0.0013	0.98	0.3224		0.0016 $\pm$ 0.0013	1.53	0.2164		
	$P_3$	0.00002 $\pm$ 0.00001	5.07	0.0244	-0.000005 $\pm$ 0.000011	0.24	0.6235		-0.000006 $\pm$ 0.00000	0.35	0.5549		
Larva IV	$P_0$	0.7656 $\pm$ 0.1925	15.82	< 0.0001	1.6980 $\pm$ 0.1826	86.48	< 0.0001		1.7117 $\pm$ 0.2424	49.88	< 0.0001		
	$P_1$	0.0275 $\pm$ 0.0087	9.92	0.0016	-0.0396 $\pm$ 0.0065	37.58	< 0.0001		-0.0362 $\pm$ 0.0131	7.70	0.0055		
	$P_2$	-0.00036 $\pm$ 0.00009	16.30	< 0.0001	0.00016 $\pm$ 0.00005	9.67	0.0019		0.00001 $\pm$ 0.000016	0.01	0.9358		
	$P_3$	-	-	-	-	-	-		-	-	-		
Female	$P_0$	1.8304 $\pm$ 0.1680	118.8	< 0.0001	3.5677 $\pm$ 0.1821	384.0	< 0.0001		4.9041 $\pm$ 0.2884	289.13	< 0.0001		
	$P_1$	0.0211 $\pm$ 0.0034	37.75	< 0.0001	-0.0261 $\pm$ 0.0023	132.2	< 0.0001		-0.0479 $\pm$ 0.0041	138.00	< 0.0001		
	$P_2$	-0.00013 $\pm$ 0.00002	83.58	< 0.0001	-	-	-		-	-	-		
	$P_3$	-	-	-	-	-	-		-	-	-		
Male	$P_0$	0.2032 $\pm$ 0.1965	1.07	0.3010	4.6727 $\pm$ 0.6214	56.54	< 0.0001		4.6458 $\pm$ 0.5138	81.75	< 0.0001		
	$P_1$	0.1009 $\pm$ 0.0104	93.68	< 0.0001	-0.1402 $\pm$ 0.0362	14.98	0.0001		-0.0706 $\pm$ 0.0182	15.02	0.0001		
	$P_2$	-0.00109 $\pm$ 0.00015	55.49	< 0.0001	0.0023 $\pm$ 0.0007	12.61	0.0004		0.0002 $\pm$ 0.00016	1.68	0.1948		
	$P_3$	0.000003 $\pm$ 0.0000006	29.92	< 0.0001	-0.00001 $\pm$ 0.000004	13.88	0.0002		-	-	-		

$\chi^2$ : Chi-square, P: p-value

**Table 2.** Maximum likelihood estimates ( $\pm$  SE) of the logistic regression parameters representing proportion of different stages of *Tetranychus urticae* consumed by different stages of *Orius albidipennis* as a function of initial prey density.

Predator stages	Parameters	Egg			Protonymph			Female		
		Estimates	$\chi^2$	P	Estimates	$\chi^2$	P	Estimates	$\chi^2$	P
<b>Nymph I</b>	$P_0$	-0.9123 $\pm$ 0.2315	15.54	<0.0001	0.7752 $\pm$ 0.3209	5.84	0.0157	-0.5895 $\pm$ 0.2895	4.15	0.0417
	$P_1$	0.0329 $\pm$ 0.0130	6.38	0.0116	-0.1313 $\pm$ 0.0415	10.00	0.0016	-0.0748 $\pm$ 0.0275	7.41	0.0065
	$P_2$	-0.00062 $\pm$ 0.00016	14.08	0.0002	0.0021 $\pm$ 0.0014	2.42	0.1201	0.0006 $\pm$ 0.0005	1.46	0.2276
	$P_3$	-	-	-	-0.00001 $\pm$ 0.00001	1.05	0.3052	-	-	-
<b>Nymph II</b>	$P_0$	0.6400 $\pm$ 0.3278	3.81	0.0509	0.4730 $\pm$ 0.2038	5.39	0.0203	0.9623 $\pm$ 0.4047	5.66	0.0174
	$P_1$	0.1003 $\pm$ 0.0382	6.88	0.0087	-0.0559 $\pm$ 0.0126	19.75	<0.0001	-0.1483 $\pm$ 0.0673	4.85	0.0276
	$P_2$	-0.0042 $\pm$ 0.0012	12.18	0.0005	0.00036 $\pm$ 0.00017	4.85	0.0277	0.0032 $\pm$ 0.0029	1.23	0.2683
	$P_3$	0.000036 $\pm$ 0.00001	11.40	0.0007	-	-	-	-0.00003 $\pm$ 0.00004	0.65	0.4199
<b>Nymph III</b>	$P_0$	0.8202 $\pm$ 0.2217	13.69	0.0002	1.4327 $\pm$ 0.2239	40.94	<0.0001	1.5178 $\pm$ 0.3389	20.06	<0.0001
	$P_1$	0.0376 $\pm$ 0.0126	8.90	0.0029	-0.0484 $\pm$ 0.0125	14.92	0.0001	-0.1058 $\pm$ 0.0395	7.18	0.0074
	$P_2$	-0.0008 $\pm$ 0.0002	25.42	<0.0001	0.00016 $\pm$ 0.00016	1.09	0.2965	0.0014 $\pm$ 0.0013	1.26	0.2617
	$P_3$	-	-	-	-	-	-	-0.000008 $\pm$ 0.00001	0.49	0.4852
<b>Nymph IV</b>	$P_0$	0.7732 $\pm$ 0.2102	13.53	0.0002	1.9658 $\pm$ 0.1941	102.6	<0.0001	1.8776 $\pm$ 0.2412	60.61	<0.0001
	$P_1$	0.0660 $\pm$ 0.0100	43.85	<0.0001	-0.0422 $\pm$ 0.0068	38.47	<0.0001	-0.0673 $\pm$ 0.0132	26.10	<0.0001
	$P_2$	-0.0008 $\pm$ 0.0001	61.45	<0.0001	0.00013 $\pm$ 0.00006	5.69	0.0170	0.00037 $\pm$ 0.00016	5.10	0.0239
	$P_3$	-	-	-	-	-	-	-	-	-
<b>Nymph V</b>	$P_0$	1.1514 $\pm$ 0.3093	13.86	0.0002	4.1141 $\pm$ 0.3142	171.5	<0.0001	2.0585 $\pm$ 0.2595	62.95	<0.0001
	$P_1$	0.0972 $\pm$ 0.0254	14.69	0.0001	-0.0896 $\pm$ 0.0099	82.24	<0.0001	-0.0452 $\pm$ 0.0137	10.88	0.0010
	$P_2$	-0.0018 $\pm$ 0.0005	10.67	0.0011	0.00043 $\pm$ 0.00007	33.61	<0.0001	0.000077 $\pm$ 0.00017	0.22	0.6421
	$P_3$	0.000008 $\pm$ 0.000003	6.65	0.0099	-	-	-	-	-	-
<b>Female</b>	$P_0$	1.5072 $\pm$ 0.2496	36.47	<0.0001	8.8942 $\pm$ 1.6161	30.29	<0.0001	4.9067 $\pm$ 0.7348	44.58	<0.0001
	$P_1$	0.0793 $\pm$ 0.0095	69.46	<0.0001	-0.3248 $\pm$ 0.0835	15.13	0.0001	-0.0695 $\pm$ 0.0325	4.57	0.0325
	$P_2$	-0.00086 $\pm$ 0.000095	81.16	<0.0001	0.0054 $\pm$ 0.0014	15.88	<0.0001	0.00011 $\pm$ 0.00035	0.11	0.7435
	$P_3$	0.000002 $\pm$ 0.0000003	64.43	<0.0001	-0.00003 $\pm$ 0.000007	18.59	<0.0001	-	-	-
<b>Male</b>	$P_0$	-0.5824 $\pm$ 0.1441	16.34	<0.0001	3.9636 $\pm$ 0.4080	94.36	<0.0001	2.1273 $\pm$ 0.2880	54.56	<0.0001
	$P_1$	0.1098 $\pm$ 0.0043	645.68	<0.0001	-0.0660 $\pm$ 0.0151	19.12	<0.0001	-0.0142 $\pm$ 0.0149	0.90	0.0343
	$P_2$	-0.00070 $\pm$ 0.000024	874.79	<0.0001	0.0003 $\pm$ 0.00013	4.62	0.0315	-0.00033 $\pm$ 0.00018	3.48	0.0620
	$P_3$	-	-	-	-	-	-	-	-	-

$\chi^2$ : Chi-square, P: p-value

**Table 3.** Estimate ( $\pm$  SE) of instantaneous attack rate and handling time of *S. gilvifrons* on different stages of *T. urticae* (with 95% confidence limits).

Predator Stages	Prey stages											
	Egg			Protonymph			Female					
	$b^*$ ( $h^{-1}$ )	$T_h$ (h)	$T/T_h$	$r^2$	$\alpha$ ( $h^{-1}$ )	$T_h$ (h)	$T/T_h$	$r^2$	$\alpha$ ( $h^{-1}$ )	$T_h$ (h)	$T/T_h$	$r^2$
<b>Larva I</b>	0.0017 $\pm$ 0.0002 (0.0014–0.0020)	1.8386 $\pm$ 0.0479 (1.7430–1.9342)	13.05	0.98	0.0519 $\pm$ 0.0146 (0.0228–0.0811)	5.3424 $\pm$ 0.3450 (4.6540–6.0308)	4.49	0.89	0.0475 $\pm$ 0.0162 (0.0151–0.0799)	9.1857 $\pm$ 0.7198 (7.7449–10.6265)	2.61	0.87
<b>Larva II</b>	0.0052 $\pm$ 0.0008 (0.0037–0.0068)	1.0171 $\pm$ 0.0311 (0.9551–1.0790)	23.60	0.97	0.0715 $\pm$ 0.0128 (0.0459–0.0971)	2.3666 $\pm$ 0.1111 (2.1449–2.5884)	10.1	0.96	0.1039 $\pm$ 0.0231 (0.0576–0.1502)	2.9332 $\pm$ 0.1473 (2.6384–3.2281)	8.18	0.95
<b>Larva III</b>	0.0057 $\pm$ 0.0008 (0.0040–0.0073)	0.7243 $\pm$ 0.0243 (0.6758–0.7728)	33.14	0.98	0.0761 $\pm$ 0.0137 (0.0488–0.1035)	0.9584 $\pm$ 0.0738 (0.8111–1.1057)	25.0	0.96	0.1007 $\pm$ 0.0170 (0.0667–0.1347)	1.4316 $\pm$ 0.0638 (1.3043–1.5589)	16.76	0.97
<b>Larva IV</b>	0.0036 $\pm$ 0.0003 (0.0029–0.0043)	0.3830 $\pm$ 0.0127 (0.3577–0.4083)	62.66	0.99	0.0855 $\pm$ 0.0113 (0.0630–0.1080)	0.5647 $\pm$ 0.0324 (0.5004–0.6290)	42.5	0.98	0.1220 $\pm$ 0.0234 (0.0753–0.1688)	0.8172 $\pm$ 0.0514 (0.7145–0.9198)	29.37	0.97
<b>Female</b>	0.0036 $\pm$ 0.0002 (0.0032–0.0041)	0.1564 $\pm$ 0.0019 (0.1527–0.1601)	153.5	0.99	0.1588 $\pm$ 0.0119 (0.1351–0.1825)	0.2097 $\pm$ 0.0117 (0.1865–0.2329)	114.	0.99	0.3200 $\pm$ 0.0778 (0.1651–0.4749)	0.3279 $\pm$ 0.0227 (0.2826–0.3731)	76.07	0.99
<b>Male</b>	0.0039 $\pm$ 0.0002 (0.0035–0.0044)	0.1844 $\pm$ 0.0024 (0.1797–0.1891)	130.2	0.99	0.1705 $\pm$ 0.0156 (0.1395–0.2016)	0.2568 $\pm$ 0.0127 (0.2315–0.2821)	93.4	0.99	0.3752 $\pm$ 0.0837 (0.2087–0.5418)	0.4635 $\pm$ 0.0172 (0.4293–0.4977)	51.78	0.99

\* $b$ : attack rate in type III functional response;  $\alpha$ : attack rate in type II functional response;  $T$ : 24 h;  $T_h$ : handling time;  $T/T_h$ : maximum attack rate;  $r^2$ : coefficient of determination.

**Table 4.** Estimate ( $\pm$  SE) of instantaneous attack rate and handling time of *O. albidipennis* on different stages of *T. urticae* (with 95% confidence limits).

Predator Stages	Prey stages											
	Egg		Protonymph		Female							
	$b^*$ ( $h^{-1}$ )	$T_h$ (h)	$T/T_h$	$r^2$	$a$ ( $h^{-1}$ )	$T_h$ (h)	$T/T_h$	$r^2$				
<b>Nymph I</b>	0.0023 $\pm$ 0.0002 (0.0018–0.0028)	1.5132 $\pm$ 0.0397 (1.4339–1.5924)	15.86	0.98	0.0613 $\pm$ 0.0163 (0.0288–0.0938)	3.9753 $\pm$ 0.2466 (3.4833 $\pm$ 4.4673)	6.04	0.91	0.0261 $\pm$ 0.0094 (0.0074–0.0449)	7.4086 $\pm$ 0.8859 (5.6354–9.1818)	3.24	0.79
<b>Nymph II</b>	0.0111 $\pm$ 0.0024 (0.0062–0.0159)	1.0175 $\pm$ 0.0316 (0.9545–1.0805)	23.59	0.97	0.0469 $\pm$ 0.0088 (0.0294–0.0645)	1.9167 $\pm$ 0.1373 (1.6427–2.1907)	12.52	0.94	0.0591 $\pm$ 0.0137 (0.0317–0.0865)	3.3306 $\pm$ 0.2357 (2.8587–3.8024)	7.21	0.92
<b>Nymph III</b>	0.0082 $\pm$ 0.0009 (0.0063–0.0100)	0.6975 $\pm$ 0.0144 (0.6688–0.7263)	34.40	0.99	0.1053 $\pm$ 0.0210 (0.0634–0.1473)	1.1388 $\pm$ 0.0663 (1.0065–1.2710)	21.07	0.96	0.0924 $\pm$ 0.0224 (0.0476–0.1371)	1.9288 $\pm$ 0.1131 (1.7030–2.1546)	12.44	0.94
<b>Nymph IV</b>	0.0062 $\pm$ 0.0009 (0.0044–0.0080)	0.3682 $\pm$ 0.0130 (0.3424–0.3940)	65.18	0.98	0.1549 $\pm$ 0.0305 (0.0943–0.2155)	0.7290 $\pm$ 0.0307 (0.6680–0.7899)	32.92	0.97	0.1204 $\pm$ 0.0297 (0.0613–0.1796)	1.1294 $\pm$ 0.0731 (0.9835–1.2754)	21.25	0.95
<b>Nymph V</b>	0.0050 $\pm$ 0.0006 (0.0038–0.0062)	0.2569 $\pm$ 0.0094 (0.2382–0.2756)	93.42	0.99	0.2687 $\pm$ 0.0419 (0.1855–0.3520)	0.6281 $\pm$ 0.0147 (0.5989–0.6572)	38.21	0.99	0.1611 $\pm$ 0.0555 (0.0504–0.2719)	0.8379 $\pm$ 0.0727 (0.6929–0.9830)	28.64	0.94
<b>Female</b>	0.0056 $\pm$ 0.0006 (0.0044–0.0067)	0.1786 $\pm$ 0.0019 (0.1747–0.1824)	134.1	0.99	0.3214 $\pm$ 0.0494 (0.2233–0.4195)	0.2642 $\pm$ 0.0123 (0.2398–0.2885)	91.00	0.99	0.3168 $\pm$ 0.1332 (0.0510–0.5827)	0.4340 $\pm$ 0.0476 (0.3391–0.5289)	55.30	0.97
<b>Male</b>	0.0044 $\pm$ 0.0004 (0.0037–0.0052)	0.2047 $\pm$ 0.0030 (0.1987–0.2108)	117.2	0.99	0.1617 $\pm$ 0.0195 (0.1228–0.2006)	0.3552 $\pm$ 0.0202 (0.3150–0.3954)	67.57	0.99	0.3088 $\pm$ 0.1165 (0.0762–0.5413)	0.7034 $\pm$ 0.0432 (0.6172–0.7896)	34.12	0.97

\*  $b$ : attack rate in type III functional response;  $a$ : attack rate in type II functional response;  $T$ : 24 h;  $T_h$ : handling time;  $T/T_h$ : maximum attack rate;  $r^2$ : coefficient of determination.

**Table 5.** Mean ( $\pm$  SE) daily consumption by different stages of *Stethorus gilvifrons* and *Orius albidipennis* at different densities of *Tetranychus urticae* eggs.

Predator species	Predator stages	<i>T. urticae</i> density						
		2	4	8	16	32	48	
<i>S. gilvifrons</i>	Larvae I	0.4 $\pm$ 0.52 C	0.8 $\pm$ 0.42 C	1.7 $\pm$ 0.48 C	4.60 $\pm$ 1.26 D	10.5 $\pm$ 1.08 D	11.2 $\pm$ 0.92 E	
	Larvae II	0.6 $\pm$ 0.70 BC	1.4 $\pm$ 0.97 C	6.1 $\pm$ 1.20 B	10.4 $\pm$ 1.96 C	17.9 $\pm$ 3.70 C	20.1 $\pm$ 2.85 D	
	Larvae III	1.0 $\pm$ 0.82 B	2.8 $\pm$ 0.79 B	6.2 $\pm$ 1.48 AB	12.5 $\pm$ 2.37 B	21.8 $\pm$ 4.08 B	28.0 $\pm$ 3.59 C	
	Larvae IV	1.3 $\pm$ 0.48 A	3.0 $\pm$ 0.67 A	6.0 $\pm$ 0.67 B	12.0 $\pm$ 1.63 B	24.4 $\pm$ 3.69 B	37.2 $\pm$ 4.44 B	
	Female	1.4 $\pm$ 0.52 A	3.6 $\pm$ 0.70 A	7.0 $\pm$ 0.67 A	14.2 $\pm$ 0.79 A	29.7 $\pm$ 2.54 A	44.7 $\pm$ 2.91 A	
	Male	1.3 $\pm$ 0.48 A	2.7 $\pm$ 0.48 B	5.6 $\pm$ 0.70 B	13.0 $\pm$ 0.94 AB	28.7 $\pm$ 2.67 A	46.9 $\pm$ 1.37 A	
<i>O. albidipennis</i>	Nymph I	0.3 $\pm$ 0.48 B	0.9 $\pm$ 0.32 C	2.0 $\pm$ 0.47 D	5.60 $\pm$ 1.07 D	13.4 $\pm$ 0.97 D	13.8 $\pm$ 1.40 E	
	Nymph II	1.2 $\pm$ 0.63 A	2.5 $\pm$ 1.43 AB	7.2 $\pm$ 1.48 AB	12.2 $\pm$ 2.15 C	21.6 $\pm$ 4.97 C	22.1 $\pm$ 3.54 D	
	Nymph III	1.1 $\pm$ 0.32 A	2.4 $\pm$ 0.70 AB	6.2 $\pm$ 0.79 B	13.2 $\pm$ 0.79 BC	25.3 $\pm$ 3.77 B	31.3 $\pm$ 2.50 C	
	Nymph IV	1.3 $\pm$ 0.67 A	2.5 $\pm$ 0.97 AB	6.9 $\pm$ 1.66 AB	14.1 $\pm$ 1.45 AB	26.7 $\pm$ 4.47 B	43.2 $\pm$ 4.52 B	
	Nymph V	1.3 $\pm$ 0.95 A	3.3 $\pm$ 1.06 A	7.4 $\pm$ 0.84 A	14.1 $\pm$ 2.42 AB	30.4 $\pm$ 1.84 A	45.3 $\pm$ 4.19 AB	
	Female	1.4 $\pm$ 0.52 A	3.3 $\pm$ 0.82 A	7.1 $\pm$ 0.88 AB	15.2 $\pm$ 1.14 A	31.2 $\pm$ 0.92 A	46.7 $\pm$ 1.42 A	
	Male	1.1 $\pm$ 0.88 A	2.2 $\pm$ 1.23 B	4.9 $\pm$ 0.57 C	12.1 $\pm$ 0.88 C	30.2 $\pm$ 1.93 A	46.2 $\pm$ 1.40 A	

\* Means followed by the same letter in each column are not significantly different (Duncan's Multiple Range Test,  $\alpha = 0.05$ ).

**Table 5.** Continued.

Predator species	Predator stages	<i>T. urticae</i> density						
		64	80	96	148	164	196	
<i>S. gilvifrons</i>	Larvae I	11.6 $\pm$ 1.17 E	-	-	-	-	-	
	Larvae II	23.8 $\pm$ 2.53 D	-	-	-	-	-	
	Larvae III	31.7 $\pm$ 4.32 C	-	-	-	-	-	
	Larvae IV	48.8 $\pm$ 4.32 B	52.6 $\pm$ 4.14 B	-	-	-	-	
	Female	59.3 $\pm$ 3.89 A	75.0 $\pm$ 3.33 A	90.2 $\pm$ 2.77 A	130.4 $\pm$ 4.83 A	138.4 $\pm$ 3.36 A	138.8 $\pm$ 2.59	
	Male	61.1 $\pm$ 2.64 A	75.3 $\pm$ 1.83 A	87.8 $\pm$ 3.27 A	117.0 $\pm$ 5.52 B	119.0 $\pm$ 9.64 B	-	
<i>O. albidipennis</i>	Nymph I	13.9 $\pm$ 1.52 E	-	-	-	-	-	
	Nymph II	22.8 $\pm$ 3.85 D	-	-	-	-	-	
	Nymph III	32.1 $\pm$ 2.85 C	-	-	-	-	-	
	Nymph IV	55.2 $\pm$ 6.37 B	56.9 $\pm$ 6.12 C	-	-	-	-	
	Nymph V	57.0 $\pm$ 7.92 B	71.3 $\pm$ 3.77 B	80.2 $\pm$ 6.70 B	-	-	-	
	Female	62.5 $\pm$ 1.27 A	77.0 $\pm$ 1.89 A	92.4 $\pm$ 3.36 A	121.6 $\pm$ 2.07 A	126.8 $\pm$ 11.8 A	128.8 $\pm$ 6.34	
	Male	59.0 $\pm$ 3.8 AB	74.9 $\pm$ 4.58 AB	90.2 $\pm$ 3.65 A	107.7 $\pm$ 8.88 B	108.8 $\pm$ 11.3 B	-	

\* Means followed by the same letter in each column are not significantly different (Duncan's Multiple Range Test,  $\alpha = 0.05$ ).

**Table 6.** Mean ( $\pm$  SE) daily consumption by different stages of *Stethorus gilvifrons* and *Orius albidipennis* at different densities of *Tetranychus urticae* protonymphs.

Predator species	Predator stages	<i>T. urticae</i> density									
		2	4	8	16	32	48	64	80	96	
<i>S. gilvifrons</i>	Larvae I	1.4 $\pm$ 0.84 B	2.3 $\pm$ 0.67 D	2.8 $\pm$ 1.03 D	3.10 $\pm$ 1.37 D	3.8 $\pm$ 1.55 E	4.2 $\pm$ 1.40 E	4.7 $\pm$ 1.06 E	-	-	-
	Larvae II	1.5 $\pm$ 0.53 B	3.0 $\pm$ 0.67 C	4.8 $\pm$ 1.40 C	7.10 $\pm$ 1.60 C	7.7 $\pm$ 1.64 D	8.5 $\pm$ 1.27 D	10.0 $\pm$ 2.11 D	-	-	-
	Larvae III	1.7 $\pm$ 0.48 AB	3.4 $\pm$ 0.84 BC	6.2 $\pm$ 1.23 B	11.0 $\pm$ 2.58 B	15.1 $\pm$ 2.81 C	17.9 $\pm$ 4.70 C	20.6 $\pm$ 3.69 C	-	-	-
	Larvae IV	1.7 $\pm$ 0.48 AB	3.4 $\pm$ 0.52 BC	5.7 $\pm$ 0.67 B	11.7 $\pm$ 1.57 B	22.2 $\pm$ 4.54 B	26.9 $\pm$ 3.18 B	27.7 $\pm$ 2.58 B	31.1 $\pm$ 4.09 B	35.0 $\pm$ 6.67 C	-
	Female	2.0 $\pm$ 0.00 A	4.0 $\pm$ 0.00 A	8.0 $\pm$ 0.00 A	16.0 $\pm$ 0.00 A	29.6 $\pm$ 0.70 A	42.2 $\pm$ 1.75 A	55.1 $\pm$ 2.81 A	66.8 $\pm$ 4.13 A	71.2 $\pm$ 3.12 A	-
Male	2.0 $\pm$ 0.00 A	3.9 $\pm$ 0.32 AB	7.8 $\pm$ 0.42 A	15.4 $\pm$ 0.84 A	28.0 $\pm$ 1.41 A	41.7 $\pm$ 3.27 A	53.6 $\pm$ 3.92 A	64.1 $\pm$ 2.69 A	64.2 $\pm$ 2.57 B	-	
<i>O. albidipennis</i>	Nymph I	1.3 $\pm$ 0.48 BC	2.4 $\pm$ 0.97 DC	3.5 $\pm$ 0.85 C	4.8 $\pm$ 1.93 E	5.3 $\pm$ 1.77 F	5.3 $\pm$ 1.89 G	5.8 $\pm$ 1.55 G	-	-	-
	Nymph II	1.1 $\pm$ 0.74 C	2.2 $\pm$ 0.92 D	4.1 $\pm$ 0.74 C	7.1 $\pm$ 1.52 D	8.5 $\pm$ 3.03 E	10.0 $\pm$ 2.11 F	10.6 $\pm$ 2.72 F	-	-	-
	Nymph III	1.6 $\pm$ 0.52 AB	2.9 $\pm$ 0.74 BC	5.9 $\pm$ 1.10 B	10.9 $\pm$ 1.52 C	16.9 $\pm$ 3.00 D	17.2 $\pm$ 4.24 E	17.6 $\pm$ 3.20 E	-	-	-
	Nymph IV	1.7 $\pm$ 0.48 AB	3.2 $\pm$ 1.14 B	6.4 $\pm$ 1.43 B	12.6 $\pm$ 2.67 B	23.1 $\pm$ 3.11 C	27.2 $\pm$ 5.55 D	27.8 $\pm$ 3.88 D	28.5 $\pm$ 4.01 D	29.1 $\pm$ 4.38 C	-
	Nymph V	1.9 $\pm$ 0.32 A	3.9 $\pm$ 0.32 A	7.8 $\pm$ 0.42 A	15.7 $\pm$ 0.48 A	26.0 $\pm$ 1.49 B	33.2 $\pm$ 2.30 C	34.0 $\pm$ 3.37 C	34.8 $\pm$ 4.18 C	34.7 $\pm$ 2.50 B	-
Female	2.0 $\pm$ 0.00 A	4.0 $\pm$ 0.00 A	8.0 $\pm$ 0.00 A	16.0 $\pm$ 0.00 A	30.2 $\pm$ 1.14 A	44.3 $\pm$ 2.45 A	59.2 $\pm$ 3.52 A	71.4 $\pm$ 3.72 A	71.8 $\pm$ 4.05 A	-	
Male	2.0 $\pm$ 0.00 A	3.9 $\pm$ 0.32 A	7.9 $\pm$ 0.32 A	15.8 $\pm$ 0.42 A	26.9 $\pm$ 1.66 B	39.2 $\pm$ 2.44 B	47.2 $\pm$ 3.49 B	49.3 $\pm$ 5.89 B	-	-	

\* Means followed by the same letter in each column are not significantly different (Duncan's Multiple Range Test,  $\alpha = 0.05$ ).

**Table 7.** Mean ( $\pm$  SE) daily consumption by different stages of *Stethorus gilvifrons* and *Orius albidipennis* at different densities of *Tetranychus urticae* females.

Predator species	Predator stages	<i>T. urticae</i> density									
		2	4	8	16	32	48	64	80		
<i>S. gilvifrons</i>	Larvae I	1.3 $\pm$ 0.48 C	1.5 $\pm$ 0.53 D	1.8 $\pm$ 0.63 D	2.0 $\pm$ 1.05 D	2.3 $\pm$ 0.95 E	2.9 $\pm$ 0.88 E	-	-	-	-
	Larvae II	1.5 $\pm$ 0.53 BC	2.8 $\pm$ 0.79 C	5.5 $\pm$ 1.08 C	6.3 $\pm$ 2.11 C	7.0 $\pm$ 1.05 D	7.9 $\pm$ 1.29 D	-	-	-	-
	Larvae III	1.8 $\pm$ 0.42 AB	3.6 $\pm$ 0.70 AB	5.7 $\pm$ 1.25 BC	10.9 $\pm$ 2.13 B	12.3 $\pm$ 1.49 C	13.8 $\pm$ 2.39 C	15.7 $\pm$ 2.58 D	-	-	-
	Larvae IV	1.7 $\pm$ 0.67 AB	3.3 $\pm$ 0.82 BC	6.5 $\pm$ 1.27 B	11.7 $\pm$ 2.91 B	21.3 $\pm$ 4.06 B	23.2 $\pm$ 3.49 B	23.6 $\pm$ 3.20 C	-	-	-
	Female	2.0 $\pm$ 0.00 A	4.0 $\pm$ 0.00 A	8.0 $\pm$ 0.00 A	16.0 $\pm$ 0.00 A	30.4 $\pm$ 1.07 A	43.5 $\pm$ 3.10 A	57.6 $\pm$ 3.63 A	58.6 $\pm$ 7.96 A	-	-
Male	2.0 $\pm$ 0.00 A	3.9 $\pm$ 0.32 A	7.8 $\pm$ 0.42 A	15.6 $\pm$ 0.84 A	29.3 $\pm$ 1.70 A	41.9 $\pm$ 3.54 A	45.1 $\pm$ 3.70 B	46.1 $\pm$ 5.17 B	-	-	
<i>O. albidipennis</i>	Nymph I	0.7 $\pm$ 0.67 C	1.1 $\pm$ 1.20 D	1.9 $\pm$ 1.20 E	2.7 $\pm$ 1.25 F	2.7 $\pm$ 1.16 F	2.8 $\pm$ 1.23 F	-	-	-	-
	Nymph II	1.4 $\pm$ 0.70 B	2.7 $\pm$ 0.82 C	3.2 $\pm$ 0.79 D	5.8 $\pm$ 1.75 E	6.1 $\pm$ 2.23 E	6.3 $\pm$ 0.95 F	-	-	-	-
	Nymph III	1.7 $\pm$ 0.48 AB	3.2 $\pm$ 0.79 BC	4.9 $\pm$ 1.37 C	8.8 $\pm$ 1.87 D	10.8 $\pm$ 3.55 D	10.9 $\pm$ 3.07 E	10.9 $\pm$ 2.08 D	-	-	-
	Nymph IV	1.7 $\pm$ 0.48 AB	3.2 $\pm$ 1.14 BC	6.3 $\pm$ 1.34 B	11.8 $\pm$ 2.35 C	16.5 $\pm$ 3.44 C	18.1 $\pm$ 5.17 D	18.2 $\pm$ 3.85 C	-	-	-
	Nymph V	1.8 $\pm$ 0.42 AB	3.5 $\pm$ 0.53 AB	6.9 $\pm$ 1.20 B	12.9 $\pm$ 2.73 BC	22.0 $\pm$ 4.24 B	23.9 $\pm$ 5.38 C	24.2 $\pm$ 8.50 BC	-	-	-
Female	2.0 $\pm$ 0.00 A	4.0 $\pm$ 0.00 A	8.0 $\pm$ 0.00 A	15.9 $\pm$ 0.32 A	28.7 $\pm$ 1.70 A	43.0 $\pm$ 3.37 A	45.2 $\pm$ 11.2 A	-	-	-	
Male	1.8 $\pm$ 0.42 AB	3.6 $\pm$ 0.52 AB	6.8 $\pm$ 0.92 B	13.5 $\pm$ 0.85 B	26.8 $\pm$ 2.25 A	30.3 $\pm$ 6.43 B	30.3 $\pm$ 5.12 B	-	-	-	

\* Means followed by the same letter in each column are not significantly different (Duncan's Multiple Range Test,  $\alpha = 0.05$ ).

$$N_a = N_0 \{1 - \exp[\alpha(T_h N_e - T)]\} \quad (2)$$

where  $N_e$  is the number of prey killed;  $N_0$  is the initial number of prey;  $T_h$  is the handling time; and  $T$  is the total time available for the predator. The data was analyzed using SAS software (SAS 2007). For a type III response, the attack rate was assumed to increase with the host density according to the equation  $a = (d + bN_0)/(1 + cN_0)$  (Hassell *et al.* 1977). In cases where both  $d$  and  $c$  were not significantly different from 0; the case observed in this study, it led to  $a = bN_0$  which was inserted into Equation (2). This yielded the following formula (Hassell 1978):

$$N_a = N_0 [1 - \exp(-bTN_0/1 + bT_h N_0^2)] \quad (3)$$

An iterative nonlinear least-squares regression (SAS 2007) was used to fit the random predator equation to the data. The effect of different stages of predator on the daily consumption rate of *S. gilvifrons* and *O. albidipennis* in different prey densities was analyzed by one way analysis of variance followed by Duncan's Multiple Range Test ( $P \leq 0.05$ ) (SAS 2007).

## RESULTS

The functional response curves of different stages of *S. gilvifrons* and *O. albidipennis* to eggs, protonymphs and females of *T. urticae* are shown in Figures 1–4. When different stages of both predators preyed on eggs of *T. urticae*, logistic regression had positive linear coefficient ( $P_1 > 0$ ), whereas when they preyed on nymphs and females, the linear coefficients were negative which means the percentage of prey consumed declined with increasing prey density ( $P_1 < 0$ ; Tables 1, 2). Thus, two predators displayed a type II functional response when preying on nymphs and females of *T. urticae*, and a type III response when preying on eggs.

Estimated values of handling times ( $T_h$ ) and coefficients of attack rate ( $a$ ) or alternatively  $b$  in the type III response are presented in Tables 3 and 4. The highest attack rates ( $a$ ) of both predators were recorded by adults, although it was higher for males in *S. gilvifrons* and females in *O. albidipennis*. In terms of the attack rate, there were higher differences among nymphal stages of *O. albidipennis* than larval stages of *S. gilvifrons*. The handling time of the first instar nymph of *O. albidipennis* was shorter than the first instar larva of *S. gilvifrons*, but it was longer in the higher nymphal stages (specially on protonymphs and females of *T. urticae*) and adults of *O. albidipennis* than those of *S. gilvifrons* (Tables 3, 4).

The same trend was observed for the maximum attack rates ( $T/T_h$ ) of both predators. It means that  $T/T_h$  was higher for older stages of predator on immature stages of prey. Also the first instar nymph of *O. albidipennis* attacked more prey, whereas adults and higher nymphal stages attacked less prey than those of *S. gilvifrons*. (Tables 3 and 4). Mean daily prey consumption by different stages of *S. gilvifrons* and *O. albidipennis* on eggs, protonymphs and females of *T. urticae* are presented in Tables 5 to 7. There were significant differences among different stages of each predator in all prey densities ( $P \leq 0.05$ ). The results showed that mean number of consumed prey depended on the predator's age, in a way that it increased significantly from first larval instar of the predator to the adult stage. In most densities of the prey, female predators consumed higher number of prey individuals than males. The results also indicated that *S. gilvifrons* and *O. albidipennis* consumed more eggs than protonymphs and females of *T. urticae*. The highest egg consumption was estimated to be  $138.8 \pm 2.59$  prey/day by *S. gilvifrons* female at the density of 196 eggs.

## DISCUSSION

This study revealed the effect of different stages of *S. gilvifrons* and *O. albidipennis* on their

functional response and prey consumption. The results indicated that the functional response of the two predators on *T. urticae* eggs was type III whereas it was type II for the other stages. Functional responses of different life stages of *Stethorus* spp. and *Orius* spp. are shown in Table 8. A type II functional response is described by increasing mortality through increasing prey access which reaches a plateau at higher prey densities (Holling 1959). Such a response was observed for all stages of both *S. gilvifrons* and *O. albidipennis* on *T. urticae* protonymphs and females (Figs. 1, 2). This may indicate that the predators would be more effective at lower prey densities. Therefore, for considering the biocontrol programs of *T. urticae*, both predators need to be released soon before *T. urticae* reaches high densities (Kasap and Atlihan 2011). Fathipour and Maleknia (2016) stated that many of the predators that have been successfully released as the biological control agents have shown the Type II functional response on their prey.

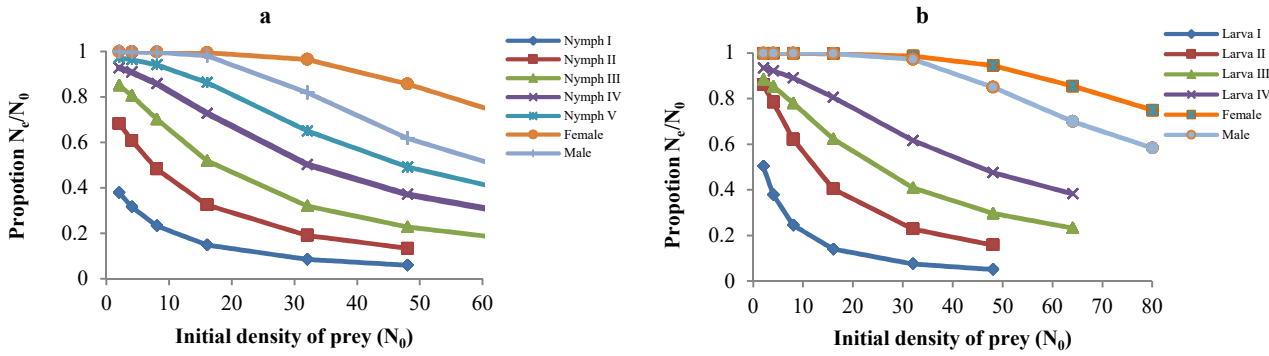
**Table 8.** Functional responses in different species of *Stethorus* and *Orius* on different preys.

Predator Species	Prey species	Temperature (°C)	Functional response	Reference
<i>Stethorus punctum</i> (LeConte) male	<i>Panonychus ulmi</i> (Koch) female	22–26 °C	II	Hull <i>et al.</i> (1977)
<i>S. punctum</i> female	<i>P. ulmi</i> female (in high densities)	22–26 °C	I	Hull <i>et al.</i> (1977)
<i>S. japonicus</i> Kamiya female	<i>T. urticae</i> (egg)	20, 25, 3° C	II	Gotoh <i>et al.</i> (2004)
<i>S. gilvifrons</i> adults	<i>T. turkestanii</i> Ugarov & Nikolski (female)	25 °C	III	Sohrabi & Shishehbor (2007)
<i>S. tridens</i> Gordon female	<i>T. evansi</i> Baker & Pritchard (nymphs)	25 °C	II	Britto <i>et al.</i> (2009)
<i>S. gilvifrons</i> female	<i>T. urticae</i> (larvae, nymph, adults)	25 °C	II	Osman (2010)
<i>S. gilvifrons</i> (all stages)	<i>Eutetranychus orientalis</i> (Klein) egg	30 °C	II	Imani and Shishehbor (2011)
<i>S. gilvifrons</i> female	<i>T. turkestanii</i> (nymphs)	25 °C	II	Karami Jamour and Shishehbor (2012)
<i>S. tridens</i> Gordon female	<i>T. bastosi</i> Tuttle (egg, larva)	27 °C	III	Costa <i>et al.</i> (2017)
<i>S. tridens</i> female	<i>T. bastosi</i> Tuttle (nymph, adults)	27 °C	II	Costa <i>et al.</i> (2017)
<b><i>S. gilvifrons</i> (all larval stages, female, male)</b>	<b><i>T. urticae</i> (egg)</b>	<b>27 °C</b>	<b>III</b>	<b>this study</b>
<b><i>S. gilvifrons</i> (all larval stages, female, male)</b>	<b><i>T. urticae</i> (protonymph, female)</b>	<b>27 °C</b>	<b>II</b>	<b>this study</b>
<i>Orius sauteri</i> (Poppius) (nymphs, adults)	<i>Thrips palmi</i> Karny (nymphs, adults)	25 °C	II	Nagai and Yano (2000)
<i>O. albidipennis</i> adults	<i>Megalurothrips sjostedti</i> larvae II and adults	15, 25, 28 °C	I and II	Gitonga <i>et al.</i> (2002)
<i>O. insidiosus</i> (Say)	<i>Helicoverpa zea</i> egg	29 °C	I	Parajulee <i>et al.</i> (2006)
<i>O. sauteri</i> adults	<i>Frankliniella occidentalis</i> (adults)	26 °C	II	Zhang <i>et al.</i> (2007)
<i>O. albidipennis</i> female	<i>Thrips tabaci</i> Lind adults	25 °C	II	Lotfi <i>et al.</i> (2008)
<i>O. albidipennis</i> female	<i>Aphis pomi</i> Degeer adults	25 °C	II	Lotfi <i>et al.</i> (2008)
<i>O. niger</i> (Wolf.) female	<i>T. urticae</i> (female)	24 °C	II	Fathi <i>et al.</i> (2010)
<i>O. minutus</i> (L.) female	<i>T. urticae</i> (female)	24 °C	II	Fathi <i>et al.</i> (2010)
<i>O. niger niger</i> female	<i>T. urticae</i> (egg)	25 °C	III	Jalalizand <i>et al.</i> (2011)
<i>O. niger niger</i> female	<i>T. urticae</i> (female)	25 °C	II	Jalalizand <i>et al.</i> (2011)
<i>O. albidipennis</i> female	<i>Tuta absoluta</i> Meyrick (egg)	26 °C	III	Salehi <i>et al.</i> (2011)
<i>O. albidipennis</i> (nymphs IV, V & adult)	<i>T. urticae</i> (egg)	26 °C	I	El-Basha <i>et al.</i> (2012)
<i>O. tricolor</i> (White) male or female	<i>Tuta absoluta</i> (Meyrick) (egg)	25 °C	II	Queiroz <i>et al.</i> (2015)
<i>O. albidipennis</i> (all stages)	<i>T. turkestanii</i> (female)	25 °C	II	Hasanzadeh <i>et al.</i> (2015)
<b><i>O. albidipennis</i>(all nymphal stages, female, male)</b>	<b><i>T. urticae</i> (egg)</b>	<b>27 °C</b>	<b>III</b>	<b>this study</b>
<b><i>O. albidipennis</i>(all nymphal stages, female, male)</b>	<b><i>T. urticae</i> (protonymph, female)</b>	<b>27 °C</b>	<b>II</b>	<b>this study</b>

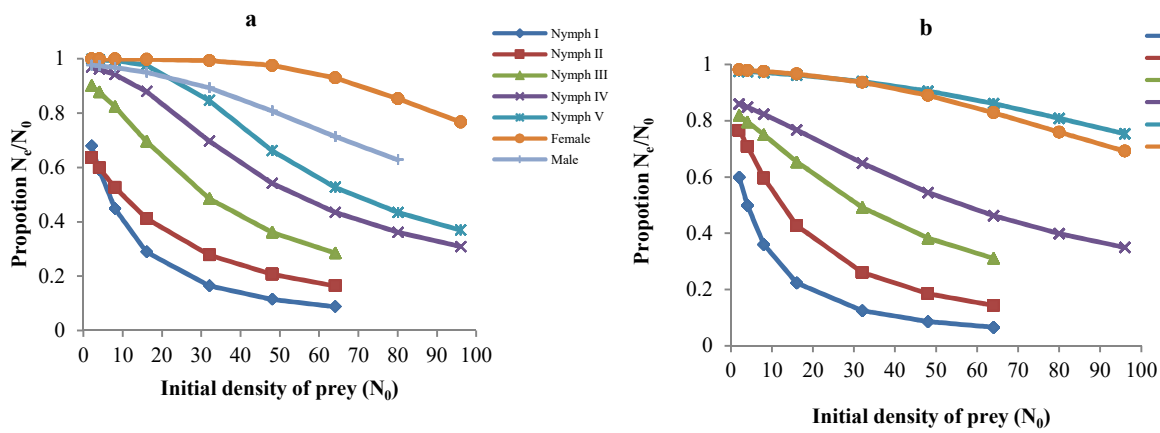
In a type III response, the predation is density-dependent, i.e. consumption of prey is low at lower densities, but increases with the prey density (Holling 1959). This response may be due to learning (searching for prey in a new environment), switching prey, or a combination of both phenomena (Holling 1959). Some predators and parasitoids show a type III response when supplied by cryptic, relatively small or immobile prey stages (Hassell 1978). Such a behavior denote situations when predator increases its rate of attack as prey density increases (Hassell 1978), which could indicate that the predator learns how to circumvent some difficulties associated to catching the prey due to increasing contact and encounter with it (Hassell 1978; Schenk & Bacher, 2002). It seems, therefore, a type III response for *S. gilvifrons* and *O. albidipennis* could be induced by the smaller size and immobility of *T. urticae* egg.

In our experiments, consumption rate of all stages of both predators was the highest on *T. urticae* eggs followed by the protonymphs and females. This finding is in agreement with Kasap and Atlihan (2011), Houck (1991), Ullah (2000), Ali *et al.* (2016), Ragkou *et al.* (2004), Ganjisaffar and Perring (2015) and Costa *et al.* (2017).

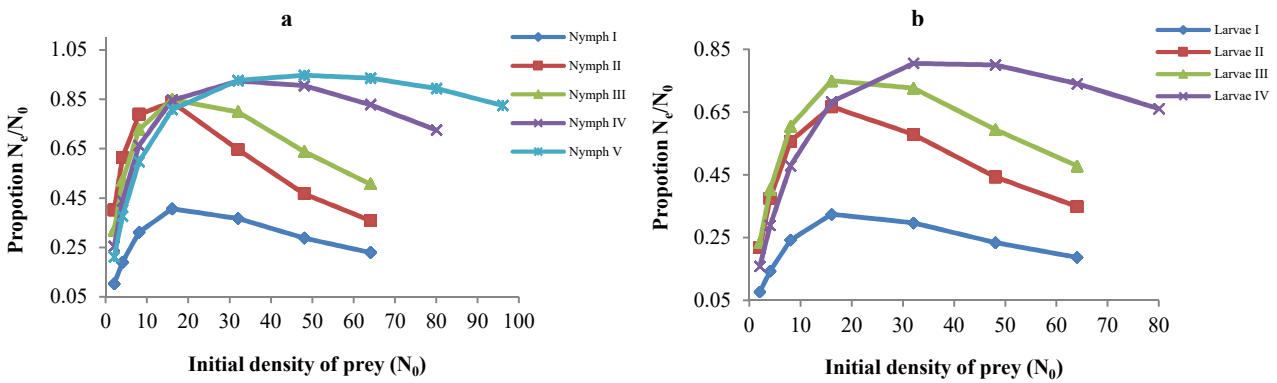
Kasap and Atlihan (2011) stated that consumption rate of predators is generally inversely related to prey size. *Stethorus* species feed on all prey life stages, but eggs usually are consumed in the largest numbers (Houck 1991; Ullah 2000). For example, Ali *et al.* (2016) found that *S. punctum* preying on *T. urticae*, consumed more immature stages than adult mites and Ragkou *et al.* (2004) reported that *S. punctillum* consumed more eggs than adults of *T. urticae*. Eggs are immobile and therefore easy to handle, but have lower biomass than other stages and therefore predators must consume more eggs to obtain the same amount of nutrients. The chorion of the egg is easier to penetrate than that of the sclerotized cuticle of nymphs and adults (Ganjisaffar and Perring 2015; Costa *et al.* 2017), which facilitates their ingestion. Also the predator takes less time to capture and kill a smaller prey than a larger one (Holling 1961). A preference for eggs is probably desirable for pest management because egg consumption prevents mites from developing and feeding on crops (Ganjisaffar and Perring 2015). In our experiments, the first instar larvae and nymphs of *S. gilvifrons* and *O. albidipennis* had the lowest daily prey consumption on all stages of *T. urticae*. The small size, slow movement and longer prey handling time of this stage could be the reasons for its lower predation rates. On the other hand, the results revealed that these two predators have different reactions to the prey stage. It means *S. gilvifrons* found female mites more rapidly than protonymphs, while this was reverse in *O. albidipennis*. Finding prey eggs has been more rapid in higher prey densities due to density dependent attack rate (type III functional response) of both predators on this prey stage. It was also longer in males than females. The handling time declined by developmental stage of both predators and increased by prey stage. According to our results, both predators exhibited suitable efficacy on different stages of *T. urticae*, but *S. gilvifrons* was more effective than the other predator and had the higher predation potential against different stages of *T. urticae* under laboratory conditions, due to higher consumption rate, shorter handling time, higher attack rate and the ability of the predator to cope with the webbing of *T. urticae*. On the other hand, *O. albidipennis* that had suitable efficacy in our experiments, may display more advantages in other circumstances; a generalist predator with lower depletion rate of prey patches may be superior for example in inoculative programs in which a long horizon of time with unpredictable events is considered or wherever other kinds of prey are present.



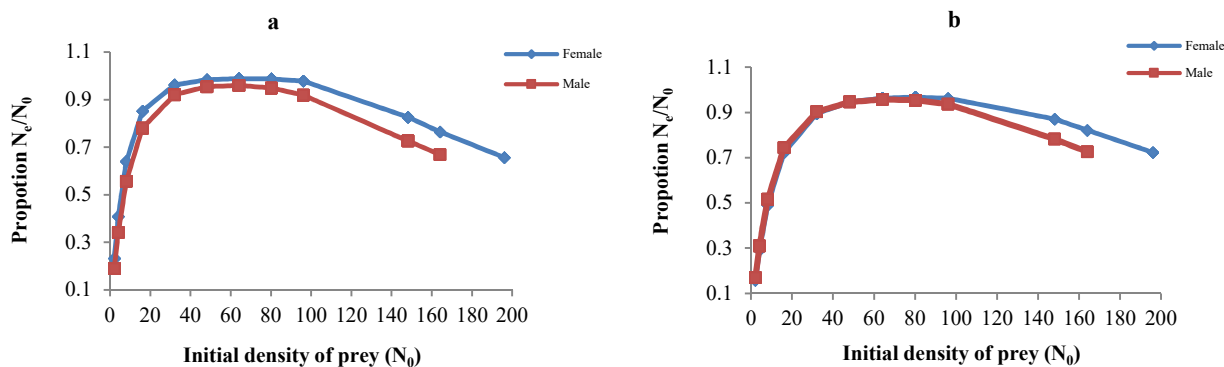
**Figure 1.** Proportion of *T. urticae* females consumed by different life stages of: a) *O. albidipennis*, b) *S. gilvifrons*, when provided by different prey densities.



**Figure 2.** Proportion of *T. urticae* protonymphs consumed by different life stages of: a) *O. albidipennis*, b) *S. gilvifrons*, when provided by different prey densities.



**Figure 3.** Proportion of *T. urticae* eggs consumed by immatures of: a) *O. albidipennis*, b) *S. gilvifrons*, when provided by different prey densities.



**Figure 4.** Proportion of *T. urticae* eggs consumed by adults of: a) *O. albidipennis*, b) *S. gilvifrons*, when provided by different prey densities.

Although functional response is an important tool for evaluating natural enemies but success or failures in biocontrol programs cannot be attributed to it alone. Other factors, such as intrinsic growth rates, host patchiness, competition, host traits, weather conditions and environmental complexities (biotic and abiotic factors) also have a major influence on the efficiency of predators in managing prey populations (Pervez and Omkar 2005). This study can help in development of appropriate control measures, although further field studies are needed to draw firm conclusions.

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مصرف روزانه و واکنش تابعی کفشدوزک *Stethorus gilvifrons* (Coleoptera: Coccinellidae) و سن شکارگر *Orius albidipennis* (Hemiptera: Anthocoridae) با تغذیه از *Tetranychus urticae* (Acari: Tetranychidae)

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#### چکیده

کنه تارتن دو لکه‌ای، *Tetranychus urticae* Koch یکی از مهمترین آفات گیاهی است که به طیف گسترده‌ای از محصولات کشاورزی در سراسر جهان خسارت وارد می‌کند. میزان مصرف و واکنش تابعی همه مراحل لاروی، افراد ماده و نر کفشدوزک *Stethorus gilvifrons* (Mulsant) و سن شکارگر *Orius albidipennis* (Reuter) به تراکم‌های مختلف تخم، پوره سن یکم و افراد ماده *T. urticae* در شرایط آزمایشگاهی ( $27 \pm 1^\circ\text{C}$ ،  $65 \pm 5\%$  رطوبت نسبی و دوره نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی) ارزیابی شد. نوع واکنش تابعی هر شکارگر توسط مدل رگرسیون لجستیک تعیین شد. از مدل راجرز برای تخمین ضریب حمله ( $a$ ) و زمان دستیابی ( $T_h$ ) استفاده شد. نتایج نشان داد که واکنش تابعی مراحل زیستی دو شکارگر روی تخم‌های کنه تارتن دو لکه‌ای از نوع سوم و روی پوره‌های سن یکم و افراد ماده این کنه از نوع دوم بود. کوتاه‌ترین زمان دستیابی ( $T_h$ ) تمام مراحل زیستی هر دو شکارگر روی تخم‌های کنه و سپس به ترتیب روی پوره‌های سن یکم و افراد ماده کنه مشاهده شدند. بیشترین و کمترین میزان حمله ( $a$ ) به ترتیب توسط افراد نر و لارو سن یکم در کفشدوزک *S. gilvifrons* و افراد ماده و پوره سن یکم در سن شکارگر *O. albidipennis* مشاهده شد. بیشترین میزان حمله روزانه ( $T/T_h$ ) روی تخم، پوره سن یکم و افراد ماده کنه تارتن دو لکه‌ای به ترتیب  $153/5$ ،  $114/4$  و  $76/07$  برای *S. gilvifrons* و  $134/1$ ،  $91$  و  $55/3$  برای *O. albidipennis* تخمین زده شدند. زمان دستیابی ( $T_h$ ) افراد کامل *S. gilvifrons* روی هر مرحله رشدی کنه تارتن دو لکه‌ای کوتاه‌تر از زمان دستیابی در افراد کامل سن شکارگر *O. albidipennis* بود. بنابر نتایج به دست آمده، هر دو شکارگر کارایی مناسب روی مراحل مختلف *T. urticae* نشان دادند، گرچه کفشدوزک *S. gilvifrons* به دلیل مصرف بیشتر، زمان دستیابی کوتاه‌تر و میزان حمله بیشتر موثرتر از سن شکارگر *O. albidipennis* در شرایط آزمایشگاهی بود.

**واژگان کلیدی:** کنترل زیستی، واکنش تابعی، شکارگر، کنه تارتن دو نقطه‌ای.

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