



## Foraging behaviour of *Scymnus syriacus* (Coleoptera: Coccinellidae) provided with *Aphis spiraecola* and *Aphis gossypii* (Hemiptera: Aphididae) as prey: Functional response and prey preference

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**Key words.** Coleoptera, Coccinellidae, Hemiptera, Aphididae, biological control, foraging behaviour, functional response, preference, switching, citrus

**Abstract.** *Scymnus syriacus* Marseul is one of the most important biocontrol agents of aphids in citrus orchards. Understanding the efficiency and host specificity of natural enemies can help improve their effectiveness as biological control agents of particular pests. In this study, the functional response, preference and switching behaviour of different stages of *S. syriacus* feeding on *Aphis spiraecola* Patch and *Aphis gossypii* Glover, on orange leaves, were studied under laboratory conditions of  $27 \pm 2^\circ\text{C}$ ,  $65 \pm 5\%$  RH and a photoperiod of 16L:8D. The results indicate that 4<sup>th</sup> instar larvae and adult males and females of this predator exhibit a type II functional response when offered different numbers (3, 5, 7, 10, 20, 30, 40, 60 and 80) of both *A. spiraecola* and *A. gossypii*. Adult females had significantly higher attack rates ( $a$ ) on both species of aphids. Handling times ( $T_h$ ) of adult male predators on *A. spiraecola* and those of 4<sup>th</sup> instar larvae on *A. gossypii* were shorter than that of the other stages. In no-choice preference experiments, adult females fed equally on both species of aphid, but the 4<sup>th</sup> instar larvae preferred *A. gossypii*. In switching experiments, prey selection was evaluated by simultaneously presenting different ratios (30:50, 40:40 and 50:30) of the two aphids, *A. spiraecola*:*A. gossypii*, to the predator. The 4<sup>th</sup> instar larvae and adult females of *S. syriacus* showed higher preference for *A. gossypii* at each ratio offered (except adult females offered the 50:30 ratio). Based on their foraging behaviour 4<sup>th</sup> instar larvae and adult females of *S. syriacus* are suitable for use in integrated management of citrus aphids.

## INTRODUCTION

Citrus is a semi-tropical fruit crop with global availability and a popular component of human diets, which is grown in more than 140 countries (Liu et al., 2012). The most common citrus fruit with commercial importance are oranges, lemons, limes, grapefruit and tangerines (Liu et al., 2012; Loghmanpour Zarini et al., 2013). There are many species of aphids that can cause economic damage in citrus orchards (Rajabi, 1986). The citrus aphid, *Aphis spiraecola* Patch and the melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) are among the aphids that attack citrus trees, especially in the north of Iran (Soroushmehr et al., 2008; Tena & Garcia-Mari, 2011; Alizadeh Kafeshani et al., 2018). Adults and immatures of these aphids can cause direct damage, especially to young citrus plantations by feeding on phloem sap. During feeding they inject saliva, which is phytotoxic and adversely affects the physiology of the trees. Furthermore, growth of sooty mould on aphid honeydew on leaves hinders their photosynthesis (Blackman & Eastop, 2000; Garzo et al., 2002). Both of these species of aphids also cause indirect damage by transmitting important viruses (Blackman & Eastop, 2000), such as

*Citrus tristeza closterovirus* (Closterovirus: Closteroviridae) (Ayazpour et al., 2013). Chemical control is the main method used to control citrus aphids (Smaili et al., 2014). However, excessive use of insecticides reduces natural enemy populations and leads to resistance of the aphids to many common insecticides. Biological control is a safe alternative method for controlling aphids in citrus orchards (Alizadeh Kafeshani et al., 2018).

*Scymnus syriacus* Marseul (Coleoptera: Coccinellidae) is a widely distributed species and is important in suppressing aphid abundance in citrus orchards (Allawi, 2006). Both larvae and adults actively search for leaves infested with aphids. They feed on many species of aphids, especially *A. spiraecola* and *A. gossypii* (Emami et al., 2004). The young larvae of *S. syriacus* usually suck out the contents of aphids, whereas adults eat the whole body of the aphids. The number of aphids consumed depends on the size of the aphid, developmental stage of the predator and environmental conditions, such as temperature. The mean number of aphids consumed by the larval stages of *S. syriacus* has reported to be 95 and 130 aphids at  $25^\circ\text{C}$  and  $30^\circ\text{C}$ , respectively (Allawi, 2006).

For the successful biological control of pests, it is necessary to understand the foraging behaviour of the natural enemies in terms of their functional response, prey preference and switching between prey (Heidarian et al., 2012; Rezaei et al., 2019). Functional response is the number of prey eaten per predator as a function of prey density (Jervis & Kidd, 1996). Holling (1959) categorized the functional response into three different types: a linear relationship between prey density and the number of prey consumed (type I), a curvilinear relationship (type II), and a sigmoidal relationship (type III). Other types of functional response, such as a dome-shaped response (type IV) and negative exponential response (type V) were reported by other researchers (Luck, 1985; Sabelis, 1992). Among these five types of functional response, type II and type III have received the most attention. Two important parameters: attack rate ( $a$ ) and handling time ( $T_h$ ) can be evaluated using functional response models. Natural enemies with high attack rate ( $a$ ) and low handling time ( $T_h$ ) are considered to be the most effective biocontrol agents (Bayoumy, 2011; Tazerouni et al., 2016).

Generalist predators may show prey preferences when foraging in patches containing more than one species of prey patches (Jaworski et al., 2013). Knowledge of the prey preferences of a predator is important for determining its predatory efficiency in situations in which various pests are present (Enkegaard et al., 2001). The tendency of a predator to choose one prey species over another may change as the relative densities of the species change (Murdoch, 1969). This behavioural trait is known as switching. Switching has a crucial role in extending the persistence of predator-prey systems (Van Baalen et al., 2001). In positive switching, a predator's preference for a specific prey increases as a function of the abundance of the prey, which could influence the stability of the prey populations. In negative switching, the predator's preference for a prey declines as a function of the abundance of this prey, and may destabilize trophic interactions by increasing the mortality of the species of prey whose density is decreasing (Murdoch, 1969; Chesson, 1984; van Baalen et al., 2001). Not all predators show switching behaviour (Chesson, 1984).

Since different types of prey have a critical effect on the foraging behaviour of predators, the present study was designed to evaluate the interactions of *S. syriacus* with two species of aphids, *A. spiraeicola* and *A. gossypii*. Thus, in the current research the functional response, prey preference and switching of *S. syriacus* between *A. spiraeicola* and *A. gossypii* reared on the leaves of orange, *Citrus sinensis* L., were investigated in order to assess the potential efficiency of this predator for controlling the abundance of aphids on citrus trees as a part of an IPM program.

## MATERIALS AND METHODS

The initial populations of *S. syriacus* and the two species of prey, *A. gossypii* and *A. spiraeicola*, were collected from unsprayed citrus orchards near Gaemshahr (36°27'47"N, 52°51'36"E), Mazandaran province, Iran. The aphids were reared on the buds of young orange trees for several generations.

The stock culture of the predator was maintained on orange leaves (*C. sinensis* cv Thomson) infested with *A. spiraeicola* or *A. gossypii* in plastic containers (9 × 10 × 21 cm) for three generations. In experiments that involved *S. syriacus* and one aphid species (functional response and no choice experiments), *S. syriacus* was reared on that aphid species. In experiments that involved *S. syriacus* and both aphid species (switching and choice experiments), the adaptation of *S. syriacus* to one species was avoided by rearing it on a mixed diet of an equal number of both species of aphids.

The experiments were conducted in Petri dishes (9 cm in diameter). Each dish had a hole (2 cm in diameter) in the lid, which was covered by fine-mesh net for ventilation and its bottom lined with a layer of solidified agar solution (2%) as a substrate to prevent orange leaves (*C. sinensis* cv. Thomson; 16.5 cm<sup>2</sup>) from desiccating. The Petri dishes were sealed with parafilm to prevent the escape of insects. All insect cultures and experiments were carried out in a growth chamber at 27 ± 2°C, 65 ± 5% RH and a photoperiod of 16L: 8D.

### Functional response experiment

This experiment was conducted with 4<sup>th</sup> instar larvae and adults (males and females less than 24 h old) of *S. syriacus* and a mixture of 3<sup>rd</sup> and 4<sup>th</sup> instar nymphs of *A. spiraeicola* or *A. gossypii*. The predators were starved for 24 h prior to the experiments by placing them individually in Petri dishes devoid of prey. Different numbers (3, 5, 7, 10, 20, 30, 40, 60, and 80) of aphids were separately offered to the different stages of the predator. After 24 h, the number of aphids eaten by the predator was recorded. For each prey density and predator stage, the experiment was replicated 10 times without prey replacement.

### Prey preference

In this study, we preferentially selected the 4<sup>th</sup> instar larvae and adult females of *S. syriacus* to study their preference and switching between *A. spiraeicola* and *A. gossypii*, because they are more voracious than adult males (Omkar & Kumar, 2013).

### No-choice experiment

In the no-choice preference assay, 1-day-old 4<sup>th</sup> instar larvae and females of *S. syriacus*, which were starved for 24 h, were used. A mixture of eighty 3<sup>rd</sup> and 4<sup>th</sup> instar nymphs of *A. spiraeicola* or *A. gossypii* were exposed to 4<sup>th</sup> instar larvae and adult females of *S. syriacus*. After 24 h, predators were removed from the arenas and the number of prey consumed was recorded. The experiment was replicated 10 times.

Independent *t*-test was used to test the significant difference between the predation rates of the predator of two species of prey (SPSS, 2007).

### Choice experiment and switching

Switching behaviour of 1-day-old 4<sup>th</sup> instar larvae and adult females of *S. syriacus* was investigated at different densities of *A. spiraeicola* or *A. gossypii* (mixture of 3<sup>rd</sup> and 4<sup>th</sup> instar nymphs). The predators were starved for 24 h before the test. *A. spiraeicola*:*A. gossypii* ratios presented to the predators were 30:50, 40:40 and 50:30. After 24 h, each predator was removed from the arena and the number of prey consumed was recorded. There were 10 replicates for each ratio of prey and developmental stage of predator.

### Statistical analyses

Statistical analysis of functional responses followed Juliano's (2001) approach. First, the type of functional response was determined using a logistic regression of the proportion of prey eaten

( $N_e$ ) as a function of prey offered ( $N_0$ ). This is done by fitting a polynomial function:

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

where  $P_0$ ,  $P_1$ ,  $P_2$  and  $P_3$  are the intercept, linear, quadratic and cubic coefficients, respectively. These coefficients were estimated using the method of maximum likelihood. If  $P_1 < 0$ , the proportion of prey eaten declines monotonically with the initial number of prey offered, which indicates a type II functional response (Juliano, 2001). If  $P_1 > 0$  and  $P_2 < 0$ , the proportion of prey eaten is initially positively dependent on the density and consequently indicates a type III functional response. After determining the type of functional response, the handling time ( $T_h$ ) and attack rate ( $a$ ) were calculated using Rogers random predator equation (Rogers, 1972) as follows:

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

where  $N_e$  is the number of prey eaten,  $N_0$  is the initial prey density,  $a$  is the attack rate,  $T_h$  is the handling time and  $T$  is the duration of the experiment. Pairwise comparisons of parameters of the functional responses for different larval instars or type of prey were performed using the indicator variable method (Juliano, 2001) as follows:

$$N_a = N_0 \{1 - \exp[-(a + D_a(j))(T - (T_h + D_{Th}(j))N_a)]\} \quad (3)$$

where  $j$  is an indicator variable that has a value of 0 for the first data set and 1 for the second data set. The parameters  $D_a$  and  $D_{Th}$  estimate the differences between the data sets being compared for the values of the parameters  $a$  and  $T_h$ , respectively. In other words, the handling time for one stage is  $T_h$ , and that for another stage is  $T_h + D_{Th}$ . Testing for a significant difference in handling times between two stages is accomplished by testing the null hypothesis that  $D_{Th}$  includes 0 (Juliano, 2001).

The maximum predation rate ( $T/T_h$ ), which is the maximum number of prey that can be consumed by a predator during 24 h, was calculated using the estimated  $T_h$  (Hassell, 2000).

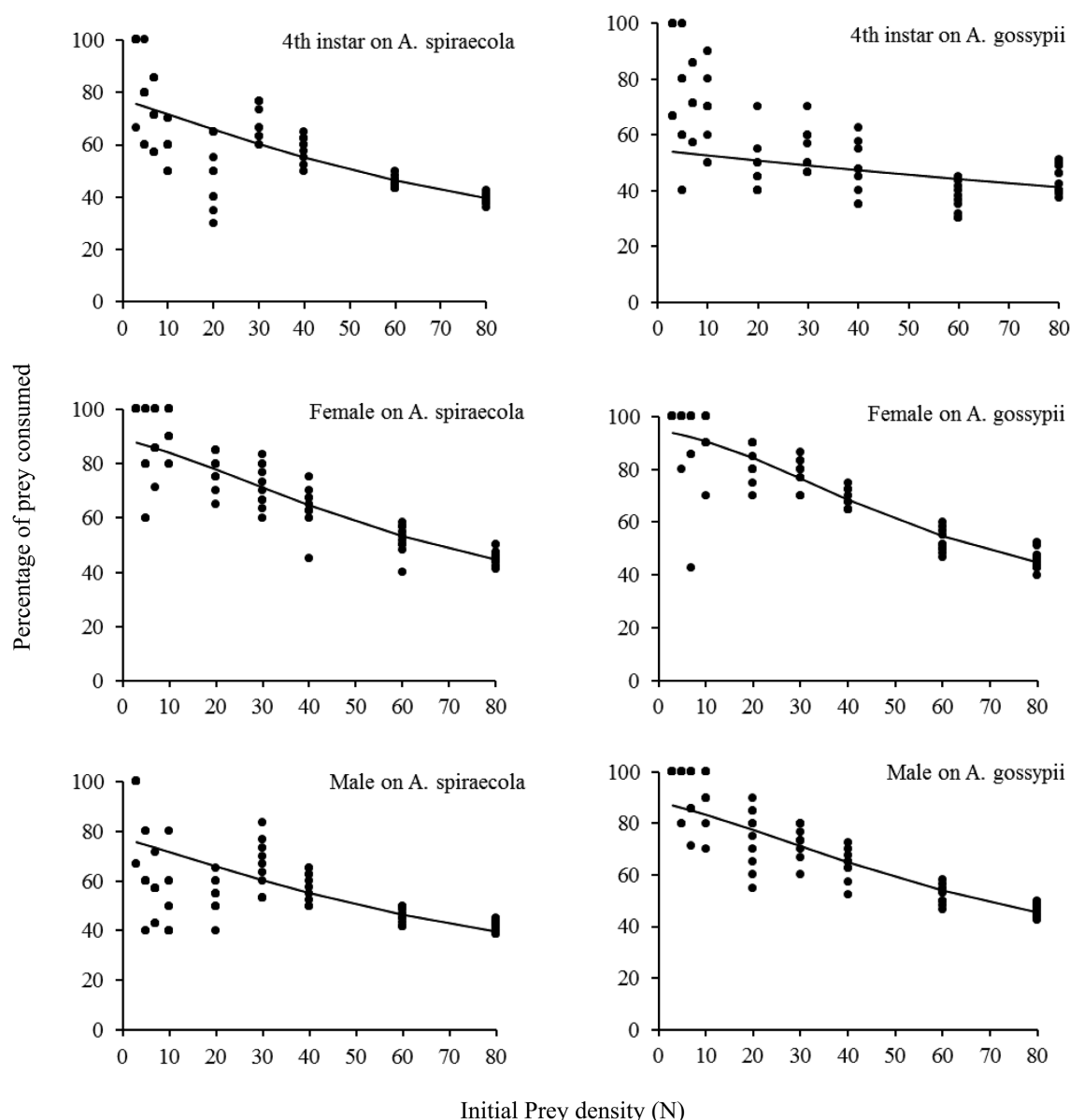
Prey preferences exhibited by 4<sup>th</sup> instar larvae and adult females of *S. syriacus* were analysed by calculating Manly's index of preference (Manly, 1974). The index was calculated using the following formula:

$$\beta_1 = \frac{\log\left(\frac{e_1}{A_1}\right)}{\log\left(\frac{e_1}{A_1}\right) + \log\left(\frac{e_2}{A_2}\right)} \quad (4)$$

where  $\beta_1$  (Beta = Manly's preference index) is the preference for a particular prey,  $e_1$  and  $e_2$  are the number of type 1 and 2 prey remaining at the end of the experiment, respectively, and  $A_1$  and  $A_2$  are the number of type 1 and 2 prey offered, respectively. The value of the index falls between 0 and 1. An index close to 1 indicates strong preference for prey type 1 and a value equal to 0.5 indicates that the predator selects prey randomly and does not show any preference. Paired *t*-test was used to test the significance of Manly's index (SPSS, 2007). It is appropriate to use this index for assays in which prey species are offered simultaneously and are not replaced during the experiment (Manly et al., 1972). To compare the number of prey eaten by each stage of predator at the mentioned ratios, one-way ANOVA followed by Tukey ( $p < 0.05$ ) test was used (SPSS, 2007). Paired *t*-test was used to compare the number of prey eaten by each stage of predator in each combination. To test the significant difference between observed (number of prey eaten) and expected values for each prey ratio, Chi-square test was used. Furthermore, to evaluate the capacity of *S. syriacus* to switch between *A. spiraeicola* and *A. gossypii*, the  $\beta$ -values were fitted to Manly's linear model for frequency dependent selection (Manly et al., 1972; Manly, 1973) as well as to non-linear models.

**Table 1.** Maximum likelihood estimates from the logistic regression analysis of the proportion of *Aphis spiraeicola* and *Aphis gossypii* consumed by 4<sup>th</sup> instar larvae and adults of *Scymnus syriacus* as a function of initial prey density.

Prey	Predator stage	Parameters	Estimate	SE	$\chi^2$	<i>p</i> -value
<i>A. spiraeicola</i>	4 <sup>th</sup> instar	Constant	0.9500	0.2368	16.09	<0.0001
		Linear	-0.0182	0.0215	0.72	0.3973
		Quadratic	0.000043	0.00054	0.01	0.9379
		Cubic	-4.52E-7	4.023E-6	0.01	0.9106
	Female	Constant	3.0138	0.3677	67.17	<0.0001
		Linear	-0.1016	0.0288	12.46	0.0004
		Quadratic	0.00122	0.000675	3.25	0.0714
		Cubic	-5.58E-6	4.719E-6	1.40	0.2373
	Male	Constant	0.2400	0.2230	1.16	0.2818
		Linear	-0.0228	0.0205	1.24	0.2661
		Quadratic	0.00078	0.000529	2.15	0.1422
		Cubic	-4.968E-6	3.9E-6	1.62	0.2027
<i>A. gossypii</i>	4 <sup>th</sup> instar	Constant	1.1963	0.2401	24.83	<0.0001
		Linear	-0.0481	0.0215	4.98	0.0257
		Quadratic	0.00025	0.00054	0.21	0.6466
		Cubic	1.541E-6	4.02E-6	0.15	0.7015
	Female	Constant	3.4145	0.4272	63.89	<0.0001
		Linear	-0.0936	0.0323	8.91	0.0028
		Quadratic	0.000847	0.00073	1.32	0.2513
		Cubic	-2.55E-6	5.077E-6	0.25	0.6157
	Male	Constant	3.3994	0.3949	74.12	<0.0001
		Linear	-0.1311	0.0303	18.74	<0.0001
		Quadratic	0.00187	0.0007	7.10	0.0077
		Cubic	-9.77E-6	4.85E-6	4.05	0.0442



**Fig. 1.** Percentage of prey consumed by 4<sup>th</sup> instar larvae and adults of *Scymnus syriacus* provided with different densities of *Aphis spiraecola* and *Aphis gossypii*. The data points and solid lines represent the percentage of prey killed and that predicted by the Rogers model, respectively.

## RESULTS

### Functional response

The results of logistic regression analyses of 4<sup>th</sup> instar larvae and adult males and females of *S. syriacus* to different numbers of *A. spiraecola* and *A. gossypii* are presented in Table 1. In all cases, the linear coefficient was negative ( $P_1 < 0$ ), indicating a type II functional response. The results revealed a decline in the proportion of the number of each prey consumed by *S. syriacus* of the initial prey density ( $N_e/N_0$ ) with increase in prey density (Fig. 1).

The attack rate ( $a$ ) and handling time ( $T_h$ ) of 4<sup>th</sup> instar larvae and adult males and females of *S. syriacus* were different for the two species of prey. Attack rate ( $a$ ) of the different stages of *S. syriacus* fed on *A. spiraecola* varied from 0.0525 to 0.0925 h<sup>-1</sup> and the estimated handling time ( $T_h$ ) ranged from 0.4165 to 0.4985 h (Table 2). Based on

the asymptotic 95% confidence interval for  $D_a$ , there were significant differences between the attack rate ( $a$ ) of adult males and adult females, and of adult females and 4<sup>th</sup> instar larvae (Table 3). It shows that the attack rate ( $a$ ) of adult females of *S. syriacus* on *A. spiraecola* is higher than that of 4<sup>th</sup> instar larvae and adult males (Table 3). Furthermore, the handling time ( $T_h$ ) of adult males on *A. spiraecola* was significantly shorter than that of adult females (Table 3).

Attack rates ( $a$ ) of different stages of *S. syriacus* fed on *A. gossypii* ranged from 0.0328 to 0.1242 h<sup>-1</sup> and their handling time ( $T_h$ ) varied from 0.2365 to 0.5362 h (Table 2). The asymptotic 95% confidence interval for  $D_a$  and  $D_{T_h}$  in pairwise comparison of various stages of *S. syriacus* fed on *A. gossypii* did not include 0, which means that there were significant differences between the attack rate ( $a$ ) and handling time ( $T_h$ ) of various stages of *S. syriacus* (Table

3). Based on the results, adult females and 4<sup>th</sup> instar larvae of *S. syriacus* had the highest and lowest attack rate ( $a$ ) on *A. gossypii*, respectively (Table 2). This trend also occurred in the values of handling time ( $T_h$ ) (Table 2).

Based on the results of pairwise comparisons, there were significant differences between the attack rate ( $a$ ) of each stage of *S. syriacus* on the two types of prey (Table 3). The attack rates of 4<sup>th</sup> instar larvae were highest on *A. spiraeicola*, whereas those of adult males and adult females were highest on *A. gossypii* (Table 2). Furthermore, the asymptotic 95% confidence interval for  $D_{Th}$  of 4<sup>th</sup> instar larvae on the two types of prey did not include 0, which means that there were significant differences between the handling times ( $T_h$ ) of 4<sup>th</sup> instar larvae of *S. syriacus* when feeding on *A. spiraeicola* and *A. gossypii* (Table 3). Based on the results, handling times on *A. gossypii* were lower (Table 2).

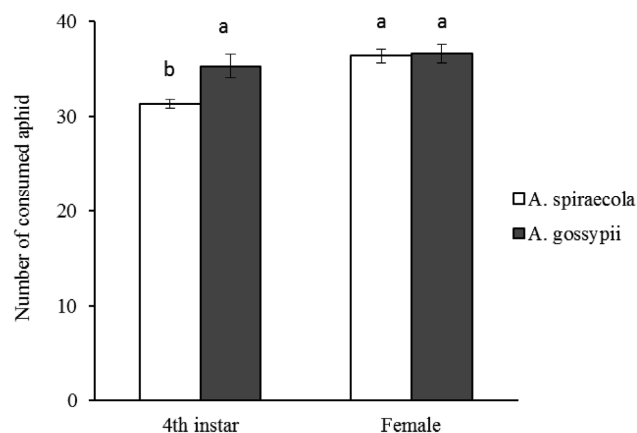
The highest maximum predation rate ( $T/T_h$ ) was recorded for adult males feeding on *A. spiraeicola* and for 4<sup>th</sup> instar larvae feeding on *A. gossypii* (Table 2). The values of the coefficient of determination ( $R^2$ ) indicated that the random predator equation adequately described the functional response of the different stages of *S. syriacus* feeding on both species of prey (Table 2).

#### No-choice preference

The mean number of prey consumed by 4<sup>th</sup> instar larvae and adult females of *S. syriacus* when provided with *A. spiraeicola* or *A. gossypii* in no-choice experiment is illustrated in Fig. 2. There was a significant difference between the number of prey consumed by 4<sup>th</sup> instar larvae ( $t = -2.961$ ;  $df = 18$ ;  $p = 0.008$ ). *A. gossypii* was more preferred than *A. spiraeicola* by 4<sup>th</sup> instar larvae. Furthermore, there was no significant difference in the number of prey consumed by adult females ( $t = -0.161$ ;  $df = 18$ ;  $p = 0.874$ ). Based on these results, the adult females of *S. syriacus* consumed significantly more *A. spiraeicola* than the 4<sup>th</sup> instar larvae ( $t = -5.762$ ;  $df = 18$ ;  $p < 0.0001$ ). However, the consumption of both adult females and 4<sup>th</sup> instar larvae of *S. syriacus* on *A. gossypii* did not differ significantly ( $t = -0.809$ ;  $df = 18$ ;  $p = 0.429$ ).

#### Choice experiment and switching

The mean numbers of prey consumed by 4<sup>th</sup> instar larvae and adult females of *S. syriacus* at different ratios of *A. spiraeicola* and *A. gossypii* are shown in Table 4. According to the results, 4<sup>th</sup> instar larvae consumed significantly more *A. spiraeicola* and *A. gossypii* at the 50 : 30 and 40 : 40 (*A. spiraeicola* : *A. gossypii*) ratios. The highest numbers of



**Fig. 2.** The mean number of aphids consumed by 4<sup>th</sup> instar larvae and adult females of *Scymnus syriacus* provided with *Aphis spiraeicola* and *Aphis gossypii* for 24 h in the no-choice experiment. Different letters indicate significant difference between the numbers of aphids consumed by each stage ( $p < 0.05$ ;  $t$  test).

*A. spiraeicola* and *A. gossypii* consumed by adult females were recorded at the 50 : 30 and 30 : 50 (*A. spiraeicola* : *A. gossypii*) ratios. At each ratio (except 50 : 30 for adult females), *A. gossypii* was significantly more preferred by both 4<sup>th</sup> instar larvae and adult females compared to *A. spiraeicola* (Table 4).

When both *A. spiraeicola* and *A. gossypii* were offered in equal numbers to the 4<sup>th</sup> instar larvae and adult females of *S. syriacus*, the Manly's preference index ( $\beta_1$ ) was significantly in favour of *A. gossypii* (Table 5). For adult females, the index for other ratios was significantly higher for *A. gossypii* than *A. spiraeicola* (Table 5). For 4<sup>th</sup> instar larvae, the preference index for the 50 : 30 ratio was higher for *A. spiraeicola* and for the 30 : 50 ratio there was no significant preference for either of the two species of aphid (Table 5).

The significant ( $F = 15.30$ ;  $df = 2, 29$ ;  $p < 0.0001$ ) and negative ( $y = -14.47x^3 + 11.85x - 4.56$ ) non-linear slope for 4<sup>th</sup> instar larvae and the significant ( $F = 19.40$ ;  $df = 1, 29$ ;  $p < 0.0001$ ) and negative ( $y = -0.549x + 0.89$ ) linear slope for adult females indicate that for the ratios of prey used, 4<sup>th</sup> instar larvae and adult females of *S. syriacus* did not switch between *A. spiraeicola* and *A. gossypii*.

## DISCUSSION

### Functional response

The results of functional response studies can determine the success or failure of biocontrol agents in inundative releases (Waage & Greathead, 1988; Heidarian et al.,

**Table 2.** Attack rate ( $a$ ), handling time ( $T_h$ ), and maximum predation rate ( $T/T_h$ ) of 4<sup>th</sup> instar larvae and adults of *Scymnus syriacus* fed on *Aphis spiraeicola* and *Aphis gossypii*. \*CI – Confidence Interval.

Prey	Predator stage	$a$		$T_h$		$T/T_h$	$R^2$
		Estimate $\pm$ SE	95% CI*	Estimate $\pm$ SE	95% CI		
<i>A. spiraeicola</i>	4 <sup>th</sup> instar	0.0618 $\pm$ 0.00451	0.0528–0.0707	0.4985 $\pm$ 0.0289	0.4410–0.5560	48.14	0.96
	Female	0.0925 $\pm$ 0.00656	0.0795–0.1055	0.4927 $\pm$ 0.0202	0.4526–0.5328	48.71	0.97
	Male	0.0525 $\pm$ 0.00362	0.0453–0.0597	0.4165 $\pm$ 0.0306	0.3557–0.4773	57.62	0.96
<i>A. gossypii</i>	4 <sup>th</sup> instar	0.0328 $\pm$ 0.0030	0.0269–0.0388	0.2365 $\pm$ 0.0585	0.1202–0.3528	101.48	0.92
	Female	0.1242 $\pm$ 0.0088	0.1066–0.1418	0.5362 $\pm$ 0.0161	0.5043–0.5681	44.76	0.98
	Male	0.0898 $\pm$ 0.0054	0.0789–0.1007	0.4737 $\pm$ 0.0177	0.4385–0.5090	50.66	0.98

**Table 3.** The parameters of the combined equation for comparing the attack rate and handling time of 4<sup>th</sup> instar larvae and adults of *Scymnus syriacus* feeding on *Aphis spiraeicola* and *Aphis gossypii*. \*CI – Confidence Interval.

Treatments	Parameter	Estimate	Standard Error	Approximate 95% CI*	
				Lower	Upper
Female / Male (on <i>A. spiraeicola</i> )	$D_a$	-0.0400	0.0076	-0.0552	-0.0248
	$D_{Th}$	-0.0762	0.0362	-0.1475	-0.0048
Female / 4 <sup>th</sup> instar (on <i>A. spiraeicola</i> )	$D_a$	0.0360	0.0091	0.0180	0.0541
	$D_{Th}$	-0.0234	0.0418	-0.0592	0.1060
Male / 4 <sup>th</sup> instar (on <i>A. spiraeicola</i> )	$D_a$	-0.0039	0.0062	-0.0163	0.0084
	$D_{Th}$	-0.0528	0.0496	-0.1507	0.0451
Female / Male (on <i>A. gossypii</i> )	$D_a$	-0.0344	0.0104	-0.0550	-0.0139
	$D_{Th}$	-0.0625	0.0239	-0.1097	-0.0153
Female / 4 <sup>th</sup> instar (on <i>A. gossypii</i> )	$D_a$	0.0914	0.0128	0.0661	0.1167
	$D_{Th}$	0.2997	0.0529	0.1954	0.4040
Male / 4 <sup>th</sup> instar (on <i>A. gossypii</i> )	$D_a$	0.0569	0.0081	0.0408	0.0730
	$D_{Th}$	0.2372	0.0539	0.1307	0.3437
4 <sup>th</sup> instar (on <i>A. gossypii</i> ) / 4 <sup>th</sup> instar (on <i>A. spiraeicola</i> )	$D_a$	0.0234	0.0061	0.0114	0.0358
	$D_{Th}$	0.2328	0.0693	0.0960	0.3696
Female (on <i>A. gossypii</i> ) / Female (on <i>A. spiraeicola</i> )	$D_a$	-0.0317	0.0113	-0.0540	-0.0094
	$D_{Th}$	-0.0436	0.0256	-0.0941	0.0070
Male (on <i>A. gossypii</i> ) / Male (on <i>A. spiraeicola</i> )	$D_a$	-0.0372	0.0069	-0.0510	-0.0235
	$D_{Th}$	-0.0572	0.0342	-0.1248	0.0103

2012). In this study, we recorded the functional responses of late instar larvae and adult male and female of *S. syriacus* to different densities of *A. spiraeicola* and *A. gossypii*, because they are much more voracious than early instar larvae (Farhadi et al., 2010). Based on the results, 4<sup>th</sup> instar larvae and adult males and females of *S. syriacus* exhibit a type II functional response to varying densities of *A. spiraeicola* and *A. gossypii*, whereby they kill an increasingly higher proportion of prey as prey density declines. Type II functional response may in part reflect the suitability of a predator for regulating orchard populations of both species of aphids (Bayoumy & Awadalla, 2018). This type of response is also reported for *S. syriacus* preying on *A. spiraeicola* (Sahragard, 1988), *Scymnus levaillanti* Mulsant on *A. gossypii* (Işıkber, 2005), *Scymnus subvilosus* Goeze on *Hyaloptera pruni* Geoffr (Atlihan & Guidal, 2009), *S. syriacus* on *A. gossypii* (Sakaki & Sahragard, 2011) and *S. syriacus* preying on *Aphis fabae* Scopoli (Sabaghi et al., 2011b). A type III functional response to different densities of the third instars nymphs of *Aphis craccivora* Koch

on broad bean, *Vicia fabae* L. leaves is also reported for *S. syriacus* females (Sabaghi et al., 2011a). This reveals that the species of prey and host plant may affect the functional response of *S. syriacus* (De Clercq et al., 2000; Sarmiento et al., 2007).

To determine the magnitude of the responses, the attack rate ( $a$ ) and handling time ( $T_h$ ) were estimated. The attack rate ( $a$ ) and handling time ( $T_h$ ) of 4<sup>th</sup> instar larvae and adult males and females of *S. syriacus* were different when feeding on the two species of prey, which implies that different stages of the predator with similar responses do not necessarily attack or handle both types of prey in a similar way (Bayoumy & Awadalla, 2018). Attack rate ( $a$ ) is the rate at which a predator searches for prey. According to the results, the attack rates ( $a$ ) of adult females foraging for both species of aphids were significantly the highest. Similarly, Sabaghi et al. (2011b) report that adult females of *S. syriacus* exhibit high attack rates ( $a$ ) when feeding on *A. fabae*. A higher attack rate ( $a$ ) means that higher numbers of prey are eaten by predators in a given time interval

**Table 4.** Mean ( $\pm$  SE) number of prey consumed by 4<sup>th</sup> instar larvae and adult females of *Scymnus syriacus* provided with different ratios of *Aphis spiraeicola* and *Aphis gossypii*.

Predator stage	Prey ratios ( <i>A. spiraeicola</i> : <i>A. gossypii</i> )	<i>A. spiraeicola</i>	<i>A. gossypii</i>	<i>t</i>	<i>df</i>	<i>p</i>
4 <sup>th</sup> instar	50 : 30	22.10 $\pm$ 1.67 <sup>Aa</sup>	12.30 $\pm$ 1.64 <sup>Bb</sup>	4.170	18	<0.0001
	40 : 40	13.70 $\pm$ 0.79 <sup>Bb</sup>	21.30 $\pm$ 0.88 <sup>Aa</sup>	-6.418	18	<0.0001
	30 : 50	11.10 $\pm$ 1.16 <sup>Bb</sup>	18.90 $\pm$ 1.24 <sup>Aa</sup>	-4.573	18	<0.0001
<i>F</i>		20.66	12.94			
<i>df</i>		2,27	2,27			
<i>p</i>		<0.0001	<0.0001			
Female	50 : 30	26.50 $\pm$ 0.95 <sup>Aa</sup>	24.50 $\pm$ 0.45 <sup>Ab</sup>	1.888	18	0.75
	40 : 40	20.50 $\pm$ 0.71 <sup>Bb</sup>	25.90 $\pm$ 1.26 <sup>Ab</sup>	-3.703	18	0.002
	30 : 50	18.20 $\pm$ 1.14 <sup>Bb</sup>	34.20 $\pm$ 0.84 <sup>Aa</sup>	-11.276	18	<0.0001
<i>F</i>		20.10	32.69			
<i>df</i>		2,27	2,27			
<i>p</i>		<0.0001	<0.0001			

Means in the same column followed by different lowercase letters are significantly different ( $p < 0.05$ , Tukey test). Means in the same row followed by different uppercase letters are significantly different ( $p < 0.05$ , *t* test).



**Table 5.** Preference index ( $\pm$  SE) of 4<sup>th</sup> instar larvae and adult females of *Scymnus syriacus* provided with different ratios of *Aphis spiraecola* and *Aphis gossypii*.

Predator stage	Prey ratios ( <i>A. spiraecola</i> : <i>A. gossypii</i> )	Preference index		<i>t</i>	<i>df</i>	<i>p</i>
		<i>A. spiraecola</i>	<i>A. gossypii</i>			
4 <sup>th</sup> instar	50 : 30	0.579 $\pm$ 0.02 <sup>A</sup>	0.420 $\pm$ 0.02 <sup>B</sup>	4.377	18	<0.0001
	40 : 40	0.356 $\pm$ 0.02 <sup>B</sup>	0.643 $\pm$ 0.02 <sup>A</sup>	-9.053	18	<0.0001
	30 : 50	0.487 $\pm$ 0.03 <sup>A</sup>	0.512 $\pm$ 0.03 <sup>A</sup>	-0.527	18	0.605
Female	50 : 30	0.309 $\pm$ 0.01 <sup>B</sup>	0.690 $\pm$ 0.01 <sup>A</sup>	-18.645	18	<0.0001
	40 : 40	0.392 $\pm$ 0.02 <sup>B</sup>	0.606 $\pm$ 0.02 <sup>A</sup>	-6.676	18	<0.0001
	30 : 50	0.447 $\pm$ 0.02 <sup>B</sup>	0.552 $\pm$ 0.02 <sup>A</sup>	-2.696	18	0.015

Means in the same row followed by different letters are significantly different ( $p < 0.05$ , *t* test).

(Jervis & Kidd, 1996). The larger size of females and their high-energy requirements for producing eggs means that adult females need to attack and consume more prey than other stages (Hodek & Honek 1996). However, the lower theoretical predation rate ( $T/T_h$ ) of females recorded in this study are due to their higher handling time ( $T_h$ ).

Handling time ( $T_h$ ) is the total time spent by a predator in catching, subduing, killing, eating and digesting prey (Veeravel & Baskaran, 1997). In this study, adult males and 4<sup>th</sup> instar larvae were significantly faster in subduing and digesting *A. spiraecola* and *A. gossypii*, respectively. Sometimes, predators that have a short handling time ( $T_h$ ) may not have a high attack rate (*a*) (Bayoumy & Awadalla, 2018). So, the inverse relationships recorded in this study between handling time ( $T_h$ ) and attack rate (*a*) in different stages of *S. syriacus* may be due to partial consumption, especially at high prey densities (Hodek & Honek, 1996; Aljetlawi et al., 2004). That is, subduing and digesting prey did not impede the predator from further searching for or handling prey. Partial consumption can result in a greater reduction in pest abundance. Pairwise comparisons revealed that adult females attacked *A. gossypii* more than *A. spiraecola*. Based on the lower handling time ( $T_h$ ) of 4<sup>th</sup> instar larvae when provided with *A. gossypii*, this stage has higher rates of maximum predation ( $T/T_h$ ). This is because of the high energy demands of its subsequent non-feeding pupal stage (Hodek & Honek, 1996). In addition, the shorter handling time ( $T_h$ ) for *A. gossypii* may be related to its smaller size compared to *A. spiraecola* (pers. observ.), which makes it more vulnerable to predation (Heydari et al., 2011). It is concluded that 4<sup>th</sup> instar larvae of *S. syriacus* are likely candidates for use in the biocontrol of *A. gossypii*. Furthermore, adult females could be more efficient if employed against infestations of both aphids in citrus orchards.

### No-choice preference

Prey preference is critical for understanding the population dynamics of predators and their ability to control the abundance of their prey. In addition, in order to optimize the mass rearing of natural enemies for use as biocontrol agents, it is important to know their preferred prey/host (Jervis & Kidd, 1996). Fourth instar larvae preferred *A. gossypii* to *A. spiraecola*. Furthermore, the number of *A. spiraecola* and *A. gossypii* consumed by adult females did not differ significantly, which indicated that the adult stage did not show a preference for either of these aphids. Butin

et al. (2004) demonstrate that *Scymnus ningshanensis* Yu & Yao show little preference (in terms of consumption) for different species of adelgids (*Adelges tsugae* Annand and *Adelges cooleyi* Gillette or *Pineus strobe* Hartig), but does not prefer the woolly alder aphid (*Paraprociphilus tessellatus* Fitch). Limbu et al. (2015) report that *Scymnus campodromus* Yu and Liu shows no preference for either the woolly alder aphid (*P. tessellatus*) or woolly apple aphid (*Eriosoma lanigerum* Hausmann) and only a slight preference for *A. gossypii* in choice and no-choice experiments.

Nutritional quality of aphids for the survival, development, weight gain, egg maturation and oviposition of predators has an important role in the prey preferences of predators (Provost et al., 2006; Jessie et al., 2015). Physiological and morphological status of host plant, predator characteristics such as age, size, hunger level, genetic traits, encounter rate and environmental conditions may also affect the prey preferences of predators (Thompson, 1975; Ferran & Dixon, 1993; Dixon 1998; Al-Zyoud & Sengonca, 2004; Provost et al., 2006; Banihashemi et al., 2017). It is possible that these traits influenced the selection of prey by *S. syriacus* in our study. However, the different ability of 4<sup>th</sup> instar larvae and adult females of *S. syriacus* in handling prey, as mentioned above, as well as different physiological characteristics of aphids may affect the prey preference of the different stages of predators.

### Choice experiment and switching

Switching behaviour is a good strategy for coping with prey scarcity (Hassanzadeh Avval et al., 2018). *S. syriacus* 4<sup>th</sup> instar larvae and adult females preferred *A. gossypii*, when two species of aphids were offered in equal proportions. However, this predator, especially the adult females, did not switch their preference from *A. gossypii* to *A. spiraecola* when the abundance of *A. spiraecola* was increased, indicating a density independent preference. Likewise, working with two coccinellids (*Coccinella septempunctata* L. and *Harmonia axyridis* Pallas) and two species of prey (*Aphis citricola* Van der Goot and *Tetranychus urticae* Koch), Lucas et al. (1997) does not report switching behaviour as both coccinellids preferred *A. citricola*. The preference for a particular species implies that the predator choose that prey independently of its abundance or accessibility (Keshavarz et al., 2015).

Generally, predators forage for food efficiently and tend to increase their nutritional gain while decreasing the costs and risks associated with predation (Stephens & Krebs,

1986). Therefore, when a predator encounters two types of prey it chooses the one most likely to maximize its fitness (higher survival, fecundity, etc.), and net energy gain (Stephens & Krebs, 1986). In this regard, large prey are more likely to be selected by predators because of their higher-energy content (Soares et al., 2004). The two species of aphids used in our experiments differed in terms of their size, i.e. *A. spiraecola* is the larger of the two. However, *S. syriacus* preferred the smaller species (i.e. *A. gossypii*) in the current study. Similarly, Keshavarz et al. (2015) report that the aphidophagous ladybird, *Propylea quatuordecimpunctata* L. prefers *A. gossypii* over *A. fabae* despite the larger size of the latter.

According to Holling (1961), predators spend more time capturing and killing large than small prey, which may decrease their capture efficiency and consumption rate. Schmidt et al. (2012) report that, even when prey size is controlled for, prey quality affects the predator's preference. Other factors such as aphid mobility, its escape behaviour (walking away, kicking), defensive secretion from abdominal cornicles, vulnerability to predators, the aphid's physical structure, such as thickness of its cuticle, length of appendages, overall body size and duration of the experiment may influence the acceptance of particular aphids by predators (Lawton et al., 1974; Crawley, 1992; Eubanks & Denno, 2000; Nedved & Salvucci, 2008). Therefore, it is necessary to determine whether and to what extent these features determined *S. syriacus* preference for *A. gossypii* over *A. spiraecola* in this study.

## CONCLUSION

The results of the current study extend our knowledge on the functional response and prey preference of one of the most important predators of citrus aphids and provide a better understanding of prey-predator interactions. This laboratory study revealed that the 4<sup>th</sup> instar larvae of *S. syriacus* were more efficient predators of *A. gossypii* and adult females more efficient predators of both *A. spiraecola* and *A. gossypii*. However, we believe that the 4<sup>th</sup> instar larvae and adult females of *S. syriacus* could act synergistically in controlling the population abundance of both of these aphids in citrus orchards, because 4<sup>th</sup> instar larvae usually remain longer in patches of aphids, and thus can be very efficient in controlling the abundance of aphids in each patch, while the adults usually fly and disperse actively and thus can find new patches of aphids (Hodek & Honek, 1996). Therefore, further field-based studies are needed in order to provide more accurate estimates of the biocontrol potential of *S. syriacus* in citrus orchards.

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