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Age-specific functional response and predation capacity of *Phytoseiulus persimilis* (Phytoseiidae) on the two-spotted spider mite

Yaghoub Fathipour^a, Maryam Karimi^a, Azadeh Farazmand^b,
Ali Asghar Talebi^a

^a Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P. O. Box 14115-336, Tehran, Iran.

^b Department of Agricultural Zoology, Iranian Research Institute of Plant Protection, Agricultural Research Education and Extension Organization (AREEO), Tehran, Iran.

ABSTRACT

The lifetime-dependent functional response and predation rate of *Phytoseiulus persimilis* Athias-Henriot on eggs of the two-spotted spider mite, *Tetranychus urticae* Koch was determined under laboratory conditions using cucumber leaf discs. Densities of 2, 4, 8, 16, 32, 64 and 128 prey were offered to 4 (protonymph), 5 (deutonymph), 6 (1-day-old adult), 10 (5-day-old adult), 15 (10-day-old adult), 20 (15-day-old adult), 25 (20-day-old adult), 30 (25-day-old adult), 35 (30-day-old adult) and 40 (35-day-old adult) *P. persimilis* individuals. The results of logistic regression analyses showed that on the 15th, 35th and 40th days of predator age, predation rate of *T. urticae* eggs increased, resulting in the type III functional response, while at the other ages, the functional response was type II. The Rogers model was used to estimate searching efficiency (*a*) and handling time (*Th*). The longest handling time was obtained in the protonymphal stage with 2.377±0.192 h. The shortest handling time and the highest value of estimated maximum attack rate (*T/Th*) were estimated at the age of 20 days (0.494±0.009 h and 48.57prey/day). At the highest prey density used (128 eggs), our findings showed that the highest number of prey was eaten by 15, 20, 25 and 30 days old *P. persimilis* (39.3, 41.7, 39.3 and 38.1 eggs per day, respectively). The results of this study revealed that *P. persimilis* especially at the middle and late ages has a good predation potential on *T. urticae* eggs at higher prey densities.

Keywords Age-specific, functional response, phytoseiid mite, *Tetranychus urticae*, two-spotted spider mite

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Corresponding author
Yaghoub Fathipour:
fathi@modares.ac.ir

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Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) is a cosmopolitan agricultural pest, feeding on more than 1100 plant species, of which more than 150 have economic value (Bolland *et al.*, 1998; Migeon *et al.*, 2011; Sedaratian *et al.*, 2011; Khanamani *et al.*, 2013; Maleknia *et al.*, 2016a).

Predatory mites in the family of Phytoseiidae have gained much attention, because of their important role in biological control of mite and insect pests, hence, there are intensive studies about the distribution, biology, ecology and behavioral characteristics of mites of this family (Fathipour and Maleknia, 2016). *Phytoseiulus persimilis* Athias-Henriot is one of the most important phytoseiid species that has been known as a very efficient biological control agent of several species of spider mites (Helle and Sabelis, 1985; Alipour *et al.*, 2016; Maleknia

et al., 2016b). According to McMurtry *et al.* (2013), this species has a type I life style and feeds exclusively on web-producing spider mites. Owing to the ability of *P. persimilis* to control spider mites, it is being mass produced and sold by many commercial biological control companies.

The performance of a predator can be affected by several attributes, two of which are the functional response and predation rate (Holling, 1959; Skalski and Gilliam, 2001). Functional response describes the relationship between a predator's consumption rate and prey density (Solomon, 1949; Holling; 1966). Several factors such as host plant traits (Cédola *et al.*, 2001; Fathipour *et al.*, 2001; Skirvin & Fenlon, 2003b; Ahn *et al.*, 2010), temperature (Skirvin and Fenlon, 2003a; Li *et al.*, 2007; Gorji *et al.*, 2009; Hoque *et al.* 2010; Jafari *et al.*, 2012), insecticides (Poletti *et al.*, 2007), prey stage (Hoque *et al.*, 2010; Farazmand *et al.*, 2012), experimental unit (Madadi *et al.*, 2011), age of a natural enemy (Asadi *et al.*, 2006; Li *et al.*, 2007; Nikbin *et al.*, 2014; Fathipour *et al.*, 2017) and generation of a natural enemy (Khanamani *et al.*, 2017) can affect functional response and its parameters.

There are many studies about functional response of *P. persimilis* (Takafuji and Chant, 1976; Everson, 1980; Fernando and Hassell, 1980; Ryoo, 1986; Sabelis and Van der Meer, 1986; Skirvin and Fenlon, 2003a; Hoque *et al.* 2010; Xiao and Fadamiro, 2010 ; Seiedy *et al.*, 2012), but none of them have focused on its age-specific functional response and predation rate. Therefore, this study aimed to reveal the searching efficiency and predation capacity of *P. persimilis* during its whole life cycle and at different life stages. Knowledge on lifetime predation capacity of a predator can help to promote its usage in biocontrol programs. On the other hand, distinguishing which stage of *P. persimilis* has the maximum attack rate and the lowest handling time can help to releasing programs.

Materials and methods

Prey culture

The specimens of *T. urticae* used in this study were obtained from the College of Agriculture, Tehran University, Iran, and reared on cucumber plants (*Cucumis sativus* cv. 'Beth Alpha') in a growth chamber at 25±1°C, 60±5% RH and a photoperiod of 16 L:8D h.

Predator source and rearing

A colony of *P. persimilis* was obtained from Koppert Biological System (Spidex®). This predator was reared in an arena consisting of a plastic sheet put on water-saturated foam in a 26×18×10 cm plastic box that was half-filled with water. The edges of the plastic sheet were covered with moist tissue paper to prevent predators from escaping (Walzer and Schausberger, 1999). Cucumber leaves infested with *T. urticae* were added to the arena three times per week.

In order to obtain predators of the same age, approximately 70-80 gravid female *P. persimilis* were randomly selected from the stock colony and transferred to a new arena before starting the experiments. The arena consisted of a piece of cucumber leaf with abundant *T. urticae* placed upside down on agar inside a 19-cm diameter Petri dish. The predatory mites were allowed to lay eggs for 12 hours, then gravid females were removed from the leaf discs. The leaf discs with the *P. persimilis* eggs were kept in a growth chamber at 25±1°C, 60±5% RH and a photoperiod of 16L:8 D hours. The experimental units were monitored until the eggs hatched. Protonymphs, deutonymphs, and different ages of adult females were used for the experiments.

Functional response

The experimental unit was a 3.5-cm diameter cucumber leaf disc that was placed upside down on a thin layer of 2% agar in a 6-cm diameter × 1-cm height Petri dish. Seven densities (2, 4, 8, 16, 32, 64 and 128) of *T. urticae* eggs were used in functional response experiments. In order

to make experimental units similar to natural conditions (i.e., presence of web and arrangement of eggs), considering the average *T. urticae* oviposition, for the above mentioned densities of *T. urticae*, 1, 2, 3, 6, 12, 22 and 44 gravid females of *T. urticae*, respectively, were transferred onto the leaf discs with a thin paintbrush, and allowed to oviposit for 24 hours and then were removed. The deposited eggs were counted, and in cases of low or high number of eggs in each density, eggs were added or removed. The predatory mites from the same-aged colony in ages 4 (protonymph), 5 (deutonymph), 6, 10, 15, 20, 25, 30, 35 and 40 days were transferred to the leaf discs with a thin paintbrush. The sex of nymphal stages was not clear, therefore mixed sexes were considered but for the adults, only females were used in the experiments.

To prevent escape of predatory mites, the 3.5 cm diameter Petri dish was sealed with parafilm. Each treatment was replicated 10 times. After 24 h the number of intact eggs remaining was counted.

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

$$\frac{N_a}{N_0} = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}{1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)} \quad (1)$$

where P_0 , P_1 , P_2 and P_3 are the intercept, linear, quadratic and cubic coefficients, respectively, estimated using the method of maximum likelihood. The sign of the P_1 from equation (1) can be used to distinguish the type of the functional response curve. If $P_1 < 0$, it describes a type II functional response. If $P_1 > 0$ and $P_2 < 0$, it shows a type III functional response (Juliano, 2001). After determining the type of functional response, the next step is to estimate the handling time and attack rate coefficients. In this study, we used an explicit deterministic model for type II functional response (Royama, 1971; Rogers, 1972):

$$N_a = N_i[1 - \exp(a(T_h N_a - T))] \quad (2)$$

where N_a is the number of prey killed, N_i is the initial number of prey, T is total time available for the predator, a is attack rate and T_h is the handling time. For a type III response, the attack rate is assumed to increase with host density according to the equation $a = (d + bN_0) / (1 + cN_0)$ (Hassell *et al.*, 1977). In cases where both d and c are not significantly different from 0, this leads to $a = bN_0$ which can be inserted into equation (2).

Then, for each host density the attack coefficient (a) can be determined as $a = bN_0$. In type III functional response, attack rate is function of prey density (N_i) and was calculated as $a' = bN_i$. An iterative nonlinear least-squares regression was used to fit the random predator equation to data so as to estimate the parameters describing the type II response. Likewise, a non-linear least squares regression procedure was used to fit the related equation to data producing a type III response.

In order to compare the effect of different densities of the prey and different ages of predator on predation rate, analysis of variance (one-way ANOVA) was used for significant differences and Tukey's test was used for means comparisons.

Results

The functional response of *P. persimilis* of different ages at different densities of *T. urticae* eggs is illustrated in Fig. 1. Comparison of functional response curves revealed profound differences between predators of different ages. The results of logistic regression analyses showed that at the age of 15, 35 and 40 days, the predation rate of *T. urticae* eggs increased, resulting in a type III functional response. The linear coefficient of equation (1) at other ages of the predator was negative and significantly different from 0 ($P < 0.01$), indicating a type II functional response

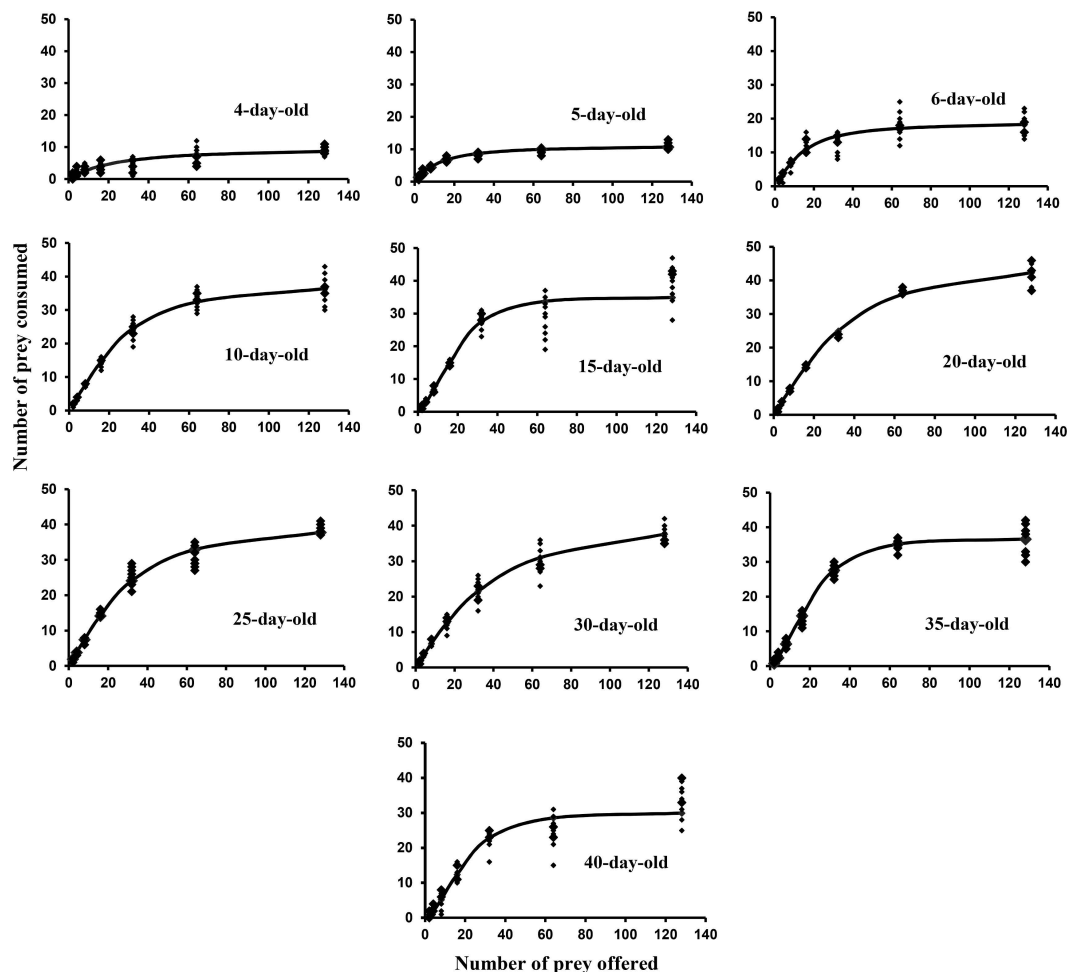


Figure 1 Age-specific functional response of *Phytoseiulus persimilis* to different densities of *Tetranychus urticae*

(Table 1). The attack rate and handling time of different ages of the predatory mite are presented in Table 2. Attack rate increased from day 4 (protonymph) up to day 10 then decreased until the last day. This parameter in type III functional response is different at each density. The maximum number of *T. urticae* eggs consumed by *P. persimilis* over a 24-h period (T/Th) was 2.02 prey per hour or 48.57 prey per day at the age of 20 day. The shortest handling time (0.49 h) was also recorded at the age of 20 days and the longest handling time was estimated to be 2.38 h for protonymphs (Table 2). Handling time, showed a significant relationship with age of *P. persimilis* ($P_{reg} = 0.009$, $R^2 = 0.903$, Fig. 2), There was a non-linear relationship (quadratic regression) between age of *P. persimilis* and handling time. So that this parameter decreased of age 4 (protonymph) up to 30th (middle age of adult) then gradually increased. Hence, at younger age (protonymph) up to middle age of adult (30 days), the slope of the regression curve was negative and thereafter with increasing age, it became positive (Fig. 2).

The number of *T. urticae* eggs consumed by *P. persimilis* at different ages and varying prey densities are displayed in Table 3. The maximum prey consumption occurred at the highest density 128 of prey for all ages and was significantly higher than other densities except at the ages of 4, 6, and 35 days when feeding was not different between the densities of 64 and 128 eggs.

Generally, at low prey densities (2 and 4 eggs), prey consumption at most ages of the predator was not significantly different. With increasing prey density (16, 32, 64 and 128

Table 1 Maximum-likelihood estimates from logistic regression of the proportion of *Tetranychus urticae* eggs consumed by different ages of *Phytoseiulus persimilis* as a function of initial prey density.

Age (day)	Parameters	Estimate (\pm SE)	χ^2	P
4	P_0	0.7994 \pm 0.2541	9.9	0.0017
	P_1	-0.1452 \pm 0.0226	41.37	<0.0001
	P_2	0.0022 \pm 0.0004	24.52	<0.0001
5	P_0	1.1189 \pm 0.2511	19.85	<0.0001
	P_1	-0.1044 \pm 0.0205	26.07	<0.0001
	P_2	0.0013 \pm 0.0004	9.71	0.0018
6	P_0	2.4425 \pm 0.3132	60.8	<0.0001
	P_1	-0.1282 \pm 0.0225	32.35	<0.0001
	P_2	0.0016 \pm 0.0004	14.48	0.0001
10	P_0	3.769 \pm 0.5131	53.96	<0.0001
	P_1	-0.1148 \pm 0.0333	11.91	0.0006
	P_2	0.0012 \pm 0.0006	4.02	0.0451
15	P_0	1.1776 \pm 0.2966	15.76	<0.0001
	P_1	0.0633 \pm 0.0232	7.45	0.0064
	P_2	-0.0020 \pm 0.0004	21.16	<0.0001
20	P_0	3.974 \pm 0.5223	57.89	<0.0001
	P_1	-0.1399 \pm 0.0337	17.24	<0.0001
	P_2	0.0018 \pm 0.0006	9.24	0.0024
25	P_0	3.528 \pm 0.5170	46.56	<0.0001
	P_1	-0.0749 \pm 0.0338	4.9	0.0268
	P_2	0.0002 \pm 0.0006	0.16	0.6862
30	P_0	2.4948 \pm 0.3521	50.21	<0.0001
	P_1	-0.073 \pm 0.0246	8.8	0.003
	P_2	0.0006 \pm 0.0004	2.02	0.1549
35	P_0	1.1269 \pm 0.3047	13.68	0.0002
	P_1	0.0773 \pm 0.0243	10.1	0.0015
	P_2	-0.00213 \pm 0.0005	20.98	<0.0001
40	P_0	0.4821 \pm 0.2561	3.54	0.0598
	P_1	0.0748 \pm 0.2561	13.72	0.0002
	P_2	-0.0021 \pm 0.0004	31.24	<0.0001

Table 2 Estimate (\pm SE) of instantaneous attack rate and handling time of *Phytoseiulus persimilis* on eggs of *Tetranychus urticae*.

Age (day)	Attack rate (a) or a'	T_h (h)	T/T_h (Prey/day)	R^2
4	0.0205 \pm 0.00374* (0.0130 - 0.0280)	2.3767 \pm 0.1918 (1.9940- 2.7594)	10.1	0.902
5	0.0544 \pm 0.00506* (0.0443 - 0.0645)	2.1026 \pm 0.0558 (1.9913 - 2.2139)	11.41	0.983
6	0.1081 \pm 0.0210* (0.0663 - 0.1500)	1.2343 \pm 0.0546 (1.1254 - 1.3432)	19.44	0.958
10	0.1562 \pm 0.0169* (0.1226 - 0.1899)	0.6008 \pm 0.0150 (0.5709 - 0.6307)	39.95	0.99
15	0.0117 \pm 0.00291** (0.00593 - 0.0176)	0.6821 \pm 0.0198 (0.6426 - 0.7216)	35.19	0.968
20	0.1301 \pm 0.00827* (0.1136 - 0.1466)	0.4941 \pm 0.00928 (0.4756 - 0.5126)	48.57	0.996
25	0.1346 \pm 0.0120* (0.1106 - 0.1586)	0.5665 \pm 0.0136 (0.5394 - 0.5936)	42.36	0.992
30	0.0885 \pm 0.00713* (0.0742 - 0.1027)	0.5334 \pm 0.0165 (0.5005 - 0.5664)	44.95	0.99
35	0.0101 \pm 0.00110** (0.00789 - 0.0123)	0.6485 \pm 0.00901 (0.6305 - 0.6665)	37	0.992
40	0.00655 \pm 0.00134** (0.00387 - 0.00923)	0.7915 \pm 0.0272 (0.7372 - 0.8458)	30.32	0.955

The values in parentheses represent 95% confidence intervals. * attack rate (a) in Type II functional, **a' (in Type III functional response) ($a'=bNt$); T_h : handling time; T/T_h : estimated maximum attack rate.

Table 3 Daily consumption of *Tetranychus urticae* eggs by *Phytoseiulus persimilis* at different ages.

Prey density	Predator age (day)										F	df	P
	4	5	6	10	15	20	25	30	35	40			
2	1.3 \pm 0.21 d AB	1.3 \pm 0.21 f AB	1.7 \pm 0.15 d A	1.9 \pm 0.10 f A	1.6 \pm 0.16 e AB	1.9 \pm 0.10 f A	1.9 \pm 0.10 f A	1.8 \pm 0.13 f A	1.6 \pm 0.16 e AB	0.9 \pm 0.27 e B	3.76	9.90	<0.0001
4	2.5 \pm 0.34 d B	3.0 \pm 0.3 e AB	3.4 \pm 0.30 cd AB	3.8 \pm 0.13 f A	3.8 \pm 0.13 de A	3.8 \pm 0.13 f A	3.7 \pm 0.15 f A	3.7 \pm 0.15 f A	3.4 \pm 0.22 e AB	2.8 \pm 0.33d e AB	3.986	9.90	<0.0001
8	3.5 \pm 0.37 bc E	4.5 \pm 0.16 d DE	5.9 \pm 0.46 c BCD	7.8 \pm 0.13 e A	7.2 \pm 0.29 d AB	7.7 \pm 0.15 e A	7.5 \pm 0.27 e AB	7.1 \pm 0.28 e ABC	6.4 \pm 0.34 d ABC	5.5 \pm 0.76 d CD	15.629	9.90	<0.0001
16	3.7 \pm 0.50 bc D	7 \pm 0.21 c C	12.7 \pm 0.62 b B	14.4 \pm 0.16 d AB	15.1 \pm 0.28 c A	14.5 \pm 0.17 d AB	15.3 \pm 0.21 d A	12.7 \pm 0.54 d B	13.8 \pm 0.53 c AB	13.6 \pm 0.67 c AB	78.713	9.90	<0.0001
32	4.7 \pm 0.67 b F	8 \pm 0.26 c E	12.9 \pm 0.92 b D	24.3 \pm 0.15 c BC	27.8 \pm 0.49 b A	23.7 \pm 0.15 c BC	25.2 \pm 0.79 c AB	21.9 \pm 0.95 c C	27.5 \pm 0.45 b A	22.6 \pm 0.86 b BC	166.122	9.90	<0.0001
64	7.5 \pm 0.79 a E	9.4 \pm 0.3 b E	17.7 \pm 1.25 a D	32.9 \pm 0.28 b AB	28.7 \pm 0.57 b B	37.2 \pm 0.25 b A	30.2 \pm 0.83 b B	30 \pm 1.24 b B	35.4 \pm 0.52 a A	23.6 \pm 1.69 b C	97.953	9.90	<0.0001
128	9.2 \pm 0.40 a E (7-11)	11.4 \pm 0.34 a E (10-13)	18.5 \pm 0.92 a D (14-23)	36.1 \pm 0.25 a BC (35-37)	39.3 \pm 0.62 a AB (36-42)	41.7 \pm 1.00 a A (37-46)	39.3 \pm 0.33 a AB (37-41)	38.1 \pm 0.67 a ABC (35-42)	36.4 \pm 1.22 a BC (30-42)	34.3 \pm 1.47 a C (25-40)	186.364	9.90	<0.0001
F	30.134	180.615	77.106	404.728	201.963	1293.894	907.018	400.239	577.931	147.82			
df	6.63	6.63	6.63	6.63	6.63	6.63	6.63	6.63	6.63	6.63			
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001			

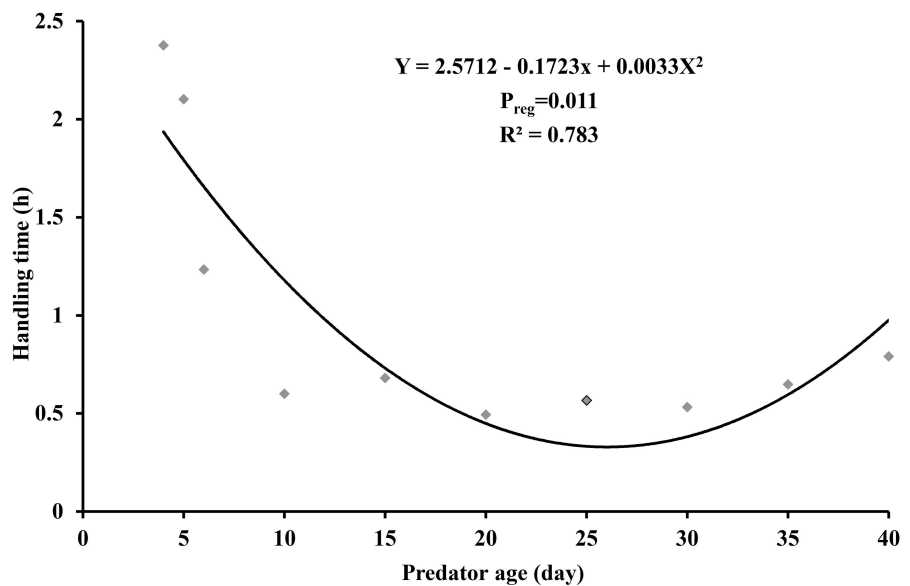


Figure 2 Quadratic regression curve between *Phytoseiulus persimilis* age and handling time on eggs of *Tetranychus urticae*

eggs), the effect of age on prey consumption was more evident. Nymphal stages (age 4 and 5 days) consumed less prey than older mites. At the beginning of maturity (6 days), prey consumption at all densities became greater with increasing age. Thereafter, mean number of prey consumption indicated fluctuation in different ages and were not significantly different in many cases. Finally, it was decreased on the 40th day of predatory mite age in all densities. The highest mean number of prey consumed, at the density of 128 eggs and at the age of 20 days, was counted to be 41.7 eggs/day (Table 3) and the lowest prey consumption was 0.9 eggs/day at the density of 2 eggs and day 40. With a density of 128 prey, the lowest prey consumption was recorded within the first three days of the experiment. Also, maximum and minimum prey consumption was 46 and 7 eggs/day recorded on the 20th and 4th days of the predatory mite age, respectively.

Discussion

Our findings revealed *P. persimilis* can show both type II and type III functional responses depending on the age of the predator supporting the hypothesis that a single predator or parasitoid species is able to exhibit different responses depending on its age. In a previous study, *A. swirskii* showed type II and III functional response at different ages (Fathipour *et al.*, 2017). Furthermore, Nikbin *et al.* (2014) and Li *et al.* (2007) obtained similar results for *Trichogramma brassicae* Bezdenko and *Scolothrips takahashii* Priesner, respectively.

Some researchers reported type II functional response for phytoseiids (Cedola *et al.*, 2001; Gotoh *et al.*, 2004; Xiao and Fadamiro, 2010; Ahn *et al.*, 2010; Gorji *et al.*, 2009; Farazmand *et al.*, 2012). In this study, immature stages of *P. persimilis* (protonymphs and deutonymphs) had a type II functional response to the density of prey eggs. This was in line with the findings of Fernando & Hassell (1980) for protonymphs and deutonymphs of *P. persimilis*. Adult females (aged 6, 10, 20, 25 and 30 days) also exhibited type II functional response. This is in agreement with Fernando & Hassell (1980) for 6-day-old adult females of *P. persimilis* and Xiao and Fadamiro (2010) for 2-9 days old adult females of this phytoseiid mite feeding on *Panonychus citri* (McGregor) nymphs. The type III functional response of 10-day-old of *P.*

persimilis can be attributed to predators having greater reproductive rates at this time interval, hence, to compensate losing energy, females consumed a significantly higher number of prey. In a study, Moghadasi *et al.* (2013) found type III functional response for gravid *P. persimilis* females aged 3 days on *T. urticae* eggs.

In this study, the type III functional response in ages of 15, 35 and 40 days of the predatory mite has been observed. However, a reason for showing type III functional response in ages of 30 and 35 days might be due to more experience of females in searching for patches with higher prey densities and oviposition strategy. In another study, Fathipour *et al.* (2017) found type III functional response for females of *Amblyseius swirskii* Athias-Henriot aged 12 days.

In our study, 20-days-old females of *P. persimilis* showed the highest estimated maximum attack rate (T/Th) (48.57) and the lowest handling time (0.49h) compared with other ages of the predatory mite and consumption rate of *P. persimilis* increased with increasing prey density. This is in line with the work of Xiao and Fadamiro (2010) who showed that *P. persimilis* consumed higher numbers of prey in particular at high prey densities and findings of Fries and Gilstrap (1982) and Hoque *et al.* (2010) who showed that prey consumption by *P. persimilis* increased significantly with increasing densities of immature prey stages. In addition, prey consumption increased from the protonymph stage up to middle age of adult females (20 day). The same trend was observed from the protonymph up to adult female stages of *P. persimilis* fed with *Tetranychus pacificus* (Eveleigh and Chant 1981) and *Typhlodromus pyri* Scheuten (Sengonca *et al.* 2003). Likewise, previous work on *A. swirskii* has shown an increasing in predation rate on *T. urticae* at the middle-age of its life and at higher prey densities (Fathipour *et al.*, 2017). The higher proportion of prey consumption at days fifteen, twenty, twenty-five, thirty, thirty-five and forty indicates that the predator would be more effective at controlling the *T. urticae* population at middle and late ages. On the other hand, the handling time showed a decreasing trend with increasing in predator age up to 30th (middle age of adult), this parameter increased again in older ages. Therefore, adult individuals at the middle and late ages are much more efficient than younger stages. This result suggests that releases of this predator may be most effective if populations can be reared and released at middle and late-stage individuals. Such releases would facilitate rapid killing of two-spotted spider mites immediately after release.

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