

Functional and numerical responses of the predator *Amblyseius swirskii* to its prey *Tetranychus turkestanii* in the laboratory

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Original research

ABSTRACT

The tetranychid *Tetranychus turkestanii* Ugarov and Nikolskii is a serious pest of many important crops around the world. Management of *T. turkestanii* by augmentative biological control using predators such as the phytoseiid *Amblyseius swirskii* (Athias-Henriot) is envisioned as an environmentally safe alternative to acaricides. Foundational knowledge on *T. turkestanii* – *A. swirskii* interactions in the laboratory are necessary to predict the outcome of *A. swirskii* augmentative releases in the field. In this study, the functional and numerical responses of adult *A. swirskii* females feeding on immature stages of *T. turkestanii* were determined in the laboratory. Prey densities were 2, 4, 8, 16, 32, 64, or 128 individuals per Petri dish arena. The functional response of *A. swirskii* to prey showed a Holling's type II response. The attack rate and handling time estimates from the random predator equation were 0.1148/h and 0.3146 h, respectively, indicating that *A. swirskii* consumed 76.28 individuals per day at the maximum level. The number of eggs laid by the predator, i.e., the numerical response, increased as host density increased up to a maximum of 33.10 eggs per female; then oviposition rate leveled-off. This study suggests that *A. swirskii* is a suitable candidate for augmentative biological control of *T. turkestanii* but follow-up experiments in greenhouses or open fields are necessary.

Keywords fecundity; Phytoseiidae; predator; rearing; spider mite; Tetranychidae

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Introduction

Tetranychus turkestanii Ugarov & Nikolskii (Acari: Tetranychidae) is an important pest of different field and glasshouse crops in the southwestern region of Iran (Mossadegh and Kocheili 2003), Russia (Popov 1981), USA (Jeppson *et al.* 1975), China (Li *et al.* 2014), India and some European countries (Zhang 2003). Characterized by frequent outbreaks coupled with acaricide resistance, this mite poses a threat to crop producers (Mossadegh and Kocheili 2003). The hosts of *T. turkestanii* are species of Solanaceae, Cucurbitaceae and Fabaceae in Khuzestan province, southwestern of Iran (Mossadegh and Kocheili 2003; Sohrabi and Shishehbor 2008). *Tetranychus turkestanii* is often found on field bindweed (*Convolvulus arvensis* L.), which may serve as a reservoir, and on several other weed species along road margins. This mite has several generations during the growing season, tolerates high temperatures and low humidity and has a short generation time of approximately 10 - 12 days (Sohrabi and Shishehbor 2008). *Tetranychus turkestanii* initially feed on the lower leaf surface but can cover an entire plant as

population density increases. Typical symptoms of *T. turkestanii* feeding are small, light colored punctures which, in prolonged exposure, develop into irregularly shaped, white or greyish-colored spots. Changes in leaf color from yellowing to bronzing are often characteristics of attack. In some host plant species, leaf curling can be a result of feeding. Necrosis may also occur in young leaves, stems and even growing tips. Sometimes leaf burning and defoliation of the host plant has been observed (Jeppson *et al.* 1975).

Amblyseius swirskii (Athias-Henriot) (Acari: Phytoseiidae) is a generalist predatory mite which consumes insects, mites, plant pollen, plant exudates, and honeydew (McMurtry *et al.* 2013). More specifically, it can develop and reproduce on psyllids (Juan-Blasco *et al.* 2012), tetranychids (Riahi *et al.* 2017a, b), eriophyids (Abou-Awad *et al.* 2000; Momen and Abdel-Khalek 2008; Park *et al.* 2010), tenuipalpids (Peña *et al.* 2009), tarsonemids (Abou-Awad *et al.* 2014; Onzo *et al.* 2012), whiteflies (Nomikou *et al.* 2001; Medd and Greatrex 2014; Shahbaz *et al.* 2019), thrips (Messelink *et al.* 2006; Wimmer *et al.* 2008), and plant pollen (Swirskii *et al.* 1967; Nomikou *et al.* 2001; Park *et al.* 2010; Lee and Gillespie 2011; Nemati *et al.* 2019). The capacity to develop and reproduce on plant pollen permits the survival of *A. swirskii* populations on plants before insect or mite infestation occurs (Calvo *et al.* 2014; Riahi *et al.* 2017 a, b). *Amblyseius swirskii* is commercially available for augmentative biological control of plant pests in more than 50 countries (Park *et al.* 2010; Calvo *et al.* 2014; Knapp *et al.* 2018). Therefore, it is a potential candidate for augmentative biological control of *T. turkestanii* in fields and greenhouses or glasshouses in Khuzestan province, southwestern Iran, and in countries where *T. turkestanii* has become invasive.

Information on functional and numerical responses of *A. swirskii* to *T. turkestanii* populations are necessary to predict the outcome of augmentative releases of *A. swirskii* against *T. turkestanii* in the field. The functional response of a predator is a function of prey density and generally follows one of three mathematical models (Holling 1959 a, b, Holling 1961). With a type I functional response model, the number of prey killed increases linearly at constant rate as a function of prey density. With a type II response model, the number of prey killed increases up to a maximum (predator saturation) but the proportion of prey killed declines with prey density. With a type III response model, predation results in a sigmoidal curve. Predators with a type III response can regulate prey populations (Holling 1965). Predators with a type II response have proven to be effective under conditions of low prey density (Koehler 1999; Krebs 1978).

The predator's numerical response is an important factor that has been attributed the success of phytoseiids in pest control (Sabelis 1985). The numerical response is a progressive change in the number of offspring in relation to prey density (Solomon 1949), and female predatory mites can vary their progeny production at different prey densities. In phytoseiid predatory mites, the numerical response is linked to the density of prey mites (Cédola *et al.* 2001; Nomikou *et al.* 2010; Carrillo and Peña 2012; Fathipour *et al.* 2020). McMurtry and Rodriguez (1987) showed that the numerical response probably had a more important role in the adjustment of pest mite populations than the functional response because increments in the numerical response, with an increase of prey density, also involved an increment in the reproduction and other important components, such as the survival of progeny and the duration of development time. The analysis of both the functional and numerical responses is helpful and provides information regarding the prey-predator relationship, which is required for the successful usage of a biological control agent.

The functional responses of *A. swirskii* feeding on an eriophyid *Aculops lycopersici* (Massee) (Park *et al.* 2010), astigmatid *Suidasia medanensis* (Oudemans) (Acari: Suidasiidae) (Midthassel *et al.* 2014), tenuipalpid *Cenopalpus irani* Dosse, and the tetranychids *Tetranychus urticae* Koch (Xiao *et al.* 2013; Fathipour *et al.* 2020) and *Eotetranychus frosti* (McGregor) (Bazgir *et al.* 2020) have been reported previously. However, no published data are available on the functional response of *A. swirskii* feeding on *T. turkestanii* (Rahmani Piyani 2021). In addition, only the numerical response of *A. swirskii* on *T. urticae* during 24 h is known (Fathipour *et al.* 2020). Therefore, the aim of this study was to determine the functional and numerical responses of *A. swirskii* feeding on *T. turkestanii*. This information will provide

baseline data necessary to predict the effectiveness of augmentative releases of *A. swirskii* to control *T. turkestanii* on crop plants in greenhouses, glasshouses, or open fields.

Material and methods

Mite colonies

Tetranychus turkestanii used in this study originated from a weed (*Convolvulus arvensis* L.) at Faculty of Agriculture, Shahid Chamran University of Ahvaz, Ahvaz, Iran. A stock colony of *T. turkestanii* was maintained on cowpea (*Vigna unguiculata* (L.) Walp.) seedlings in compost in plastic pots (20 cm diam). Infested plants were held in wooden-framed rearing cages (120 × 60 × 60 cm) covered with nylon mesh (210 µm aperture). The cages were maintained in a laboratory at 25 ± 2 °C, 60 ± 5 % RH and a 16: 8 (L: D) h with illumination (4000 lux) provided by fluorescent lamps. New plants were introduced as required to maintain the colony.

The initial population of *A. swirskii* was obtained from laboratory colonies at Bu-Ali Sina University, Hamedan, Iran, which had been purchased from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands) in 2012 and reared on *T. urticae*. Each rearing unit consisted of a plastic sheet over a foam mat maintained under humid conditions with distilled water in a Plexiglas box (17 cm × 10 cm × 6 cm). To provide food, young cowpea leaves infested with *T. turkestanii* were added to the units twice a week.

Experimental design

Experimental units were prepared according to the method described by Vantornhout *et al.* (2004) with some modifications. Each experimental unit was comprised of a green plastic sheet (3 cm × 3 cm) located on a thick foam pad, cut to a similar size (3 cm × 3 cm), in a plastic Petri dish (9 cm diam., 2 cm high) arena, half-filled with water. The edges of the plastic sheet were covered with moist tissue paper to prevent *A. swirskii* females from escaping. In addition, a few cotton threads were placed on each plastic sheet to provide shelter and oviposition substrates for *A. swirskii* females. Plant substrates were not used in the *A. swirskii* colony or in experimental units. *A. swirskii* prefers glabrous leaves (McMurtry *et al.* 2013), so we used a green plastic sheet as a substrate for experimental arenas. Besides several researchers also used plastic sheet instead of leaf to study the biology predatory behavior and rearing of phytoseiid mites (Vantornhout *et al.* 2004; Khanamani *et al.* 2016; Riahi *et al.* 2017c).

To determine the functional response of *A. swirskii*, a newly emerged female (less than 24 h old) was exposed to seven densities (2, 4, 8, 16, 32, 64 and 128) of *T. turkestanii* immature stages including larvae, protonymphs, and deutonymphs in similar proportions. Specifically, density 2 included 1 larva and 1 protonymph; density 4 included 1 larva, 1 deutonymph and 2 protonymphs; density 8 included 2 larvae, 2 deutonymphs and 4 protonymphs; density 16 included 5 larvae, 5 deutonymphs and 6 protonymphs; density 32 included 10 larvae, 10 deutonymphs and 12 protonymphs; density 64 included 20 larvae, 20 deutonymphs and 24 protonymphs; and density 128 included 40 larvae, 40 deutonymphs and 48 protonymphs. This procedure was used because our observations indicated that *A. swirskii* preferred the protonymph stage compared to other developmental stages of *T. turkestanii*. *Tetranychus turkestanii* immatures were transferred from cowpea plant foliage to Petri dish arenas using a fine paintbrush (no. 000). After 24 h, the number of dead larvae and nymphs were counted; all immature stages were combined in the final counts. Each prey density was replicated 10 times. The experiment was conducted in the laboratory at 25 ± 2 °C, 60 ± 5 % RH and a 16: 8 (L:D) h photoperiod.

In determining the numerical response, the same methods as described above were used to expose *T. turkestanii* larvae, protonymphs, and deutonymphs to *A. swirskii* females. Note that *A. swirskii* mated females were transferred into new Petri dishes containing a fresh supply of *T. turkestanii* prey, each day. Prey replacement was continued for the duration of the lifespan

of each *A. swirskii* female. The number of eggs laid by each female and its longevity was recorded every day from the beginning of the numerical response experiment until the death of each female. Each prey density was replicated 10 times. The experiment was conducted in the laboratory at 25 ± 2 °C, 60 ± 5 % RH and a 16: 8 (L:D) h photoperiod.

Statistical analysis

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) (equation 1):

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

where N_a is the number of prey attacked, N_0 is the initial density of prey, P_0 , P_1 , P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated using the maximum likelihood method. The sign of the P_1 from the above equation 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). In the next step, handling time (T_h) and attack rate (a) coefficients were estimated using the Roger's random predator equation (Rogers 1972) (equation 2):

$$N_a = N_0[1 - \exp(-aT_h N_a - T)] \quad (2)$$

where N_a and N_0 are described above, T is 24 h, the total time available for the predator, a is attack rate and T_h is the handling time. Nonlinear regression was used to estimate the attack rate and the handling time parameters (Proc NLIN, SAS Institute 2003), and the maximum predation rate was calculated from $24/T_h$.

Data on numerical response were analyzed using one-way analysis of variance (one-way ANOVA) to test whether the number of *T. turkestanii* consumed and the number of eggs laid by *A. swirskii* were different in arenas with different prey density. Statistical analysis was conducted with SAS software (SAS Institute 2003). Differences between treatment means were compared by Tukey's HSD test ($\alpha = 0.05$).

Results

Functional response

The one-way ANOVA revealed a significant effect of prey density on predation rate ($F = 14.87$; $df = 6, 63$; $P < 0.001$). The consumption rate of *A. swirskii* females increased as *T. turkestanii* density increased (Figure 1). The functional response was density-dependent and corresponded to a Holling's type II response curve (Table 1); the response increased on average from two individuals consumed a day when prey density was two *T. turkestanii* immatures to 58 individuals when prey density was 128 *T. turkestanii* immatures per arena.

The attack rate and handling time estimates from the random predator equation (equation 2) were 0.1148 h^{-1} and 0.3146 h , respectively (Table 2). The maximum number of *T. turkestanii* immatures that one *A. swirskii* female could attack was 76.28 individuals in a day.

Numerical response and longevity

Fecundity of *A. swirskii* was greatly affected by *T. turkestanii* density ($F = 40.90$; $df = 6, 63$; $P < 0.001$; Figure 2). Predators reared at the second highest prey density (64 prey per arena) produced the maximum number of eggs (33.10 eggs). Analysis of variance indicated that *T. turkestanii* density had no significant effect on longevity of *A. swirskii* females ($F = 0.54$; $df = 6, 63$; $P = 0.78$; Table 3). Mean longevity was 21.26 days (18.86 – 24.76 days).

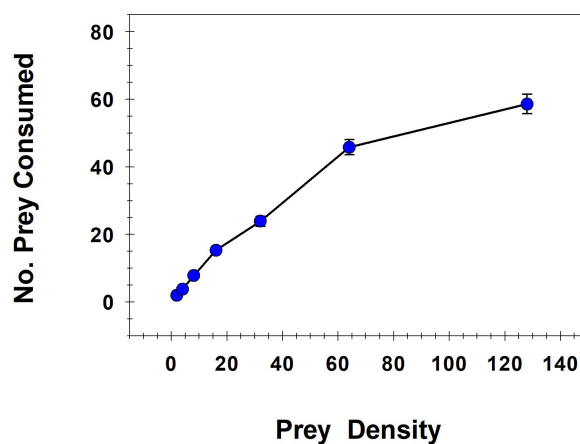


Figure 1 Mean $\pm$ SE number of *T. turkestani* immatures consumed by *A. swirskii* adult females.

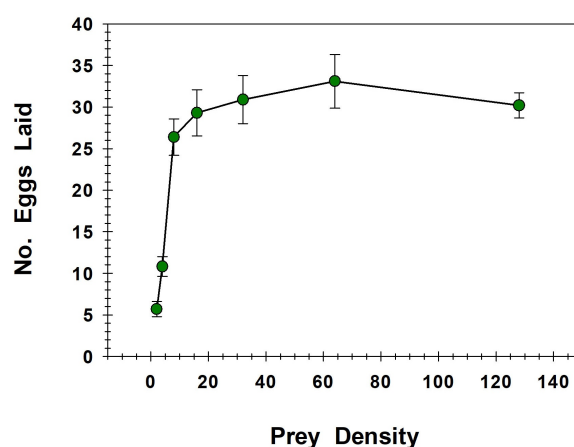


Figure 2 Numerical response, i.e., mean $\pm$ SE progeny (egg) production of *A. swirskii* females in response to different densities of *T. turkestani* immatures.

Table 1 Logistic regression analysis of the number of *T. turkestani* consumed by *A. swirskii* adult females.

Predator	Coefficient	Estimate	SE	χ^2 value	P-value
<i>A. swirskii</i>	Constant	5.5018	0.7284	57.05	< 0.0001
	Linear	-0.2357	0.0445	28.06	< 0.0001
	Quadratic	0.00363	0.000751	23.4	< 0.0001
	Cubic	-0.00002	-3.50E-06	22.7	< 0.0001

Table 2 Parameters estimated by Roger's equation for *A. swirskii* feeding on *T. turkestan*i immatures.

Parameters	Estimate	Asymptotic SE	Asymptotic 95% CI		T/T _h
			Lower	Upper	
A	0.1148 h ⁻¹	0.0163	0.0821	0.147	76.28
Th	0.3146 h	0.0197	0.2753	0.354	

Attack rate (a) and handling time (T_h).

Discussion

The functional response displayed by *A. swirskii* was well-defined by the Roger's model. The functional response curve reached a plateau at approximately 64 prey individuals during 24 h, suggesting a type II functional response where predation rate decreased as prey density increased. This type of response has been reported for *A. swirskii* on tetranychid (Xiao *et al.* 2013; Fathipour *et al.* 2017; Fathipour *et al.* 2020), tenuipalpids (Bazgir *et al.* 2020), and eriophyid (Park *et al.* 2010) mites. However, Fathipour *et al.* (2020) reported that the functional response of *A. swirskii* feeding on *T. urticae* eggs and nymphs changed to a type III response when maize pollen was provided as an additional food source.

Attack rate and handling time are two parameters that describe the magnitude of functional responses (Pervez and Omkar 2005). Handling time is an important indicator of predator effectiveness and reflects the cumulative time required for identifying, chasing, capturing, killing, and eating prey (Holling 1959 a, b, Holling 1965, Holling 1966). Different factors can influence handling time such as the speed of predator, movement of prey, and the time needed for predators to overcome individual prey (Hassell 1978), which could be related to defensive behavior of prey (Ali *et al.* 2011). The handling time found in this study (0.3146 h) was lower than the values reported for *A. swirskii* feeding on *T. urticae* eggs (0.5184 h, Xiao *et al.* 2013), *T. urticae* deutonymphs (0.9959 h, Fathipour *et al.* 2020) and *E. frosti* deutonymphs (0.8052 h, Bazgir *et al.* 2020); suggesting that *A. swirskii* had a greater predation response when feeding on a mixture of *T. turkestan*i immature stages. The shorter handling time in this study may be due to the presence of *T. turkestan*i larvae, which are easier to capture and consume in comparison to other immature prey stages. Similarly, Ganjisafar and Perring (2015) reported that the predatory mite *Galendromus flumentis* (Chant) had the shortest handling time when consuming larvae of the bank grass mite, *Oligonychus pratensis* (Banks).

In this study, *A. swirskii* females produced an average maximum number of 33.10 eggs at a prey density of 64 *T. turkestan*i immatures prey arena. Other laboratory studies with adequate densities of mature and immature stages of prey have reported a variety of fecundity (number of eggs) values for *A. swirskii*. For example, at 25 °C, Riahi *et al.* (2017 b) reported that *A. swirskii* produced an average of 40.85 eggs on *T. urticae*; Asgari *et al.* (2020) documented that *A. swirskii* produced an average of 82.17 eggs on *Carpoglyphus lactis* L. (Acari: Carpoglyphidae); Bazgir *et al.* (2018) found the average number of eggs produced by *A. swirskii* was 34.69 eggs and 25.96 eggs on *E. frosti* and *Cenopalpus irani* Dosse (Acari: Tenuipalpidae), respectively. Hosseininia *et al.* (2020) reported an average of 25.21, 21.46, and 14.87 eggs produced by *A. swirskii* feeding on *T. urticae*, *C. lactis* and *Trialeurodes vaporariorum* Westwood (Homoptera:

Table 3 Mean ± SE longevity of *Amblyseius swirskii* females fed *T. turkestan*i immatures at different densities.

Parameter	Prey density						
	2	4	8	16	32	64	128
Longevity	19.81 ± 1.58 a	20.41 ± 2.68 a	24.76 ± 2.41 a	21.36 ± 3.32 a	23.01 ± 3.43 a	20.63 ± 3.19 a	18.86 ± 2.14 a
Range	13.66-28.16	12.16-36.66	11.66-37.16	11.16-41.16	10.16-42.16	8.83-38.83	9.16-28.66

Mean values in a row followed by the same letter are not significantly different, using the Tukey HSD test at 5% significance level.

Aleyrodidae), respectively. In comparison to other studies, *A. swirskii* fecundity was moderate when fed *T. turkestanii* immatures.

The longevity of *A. swirskii* females (21.26 d) fed *T. turkestanii* in this study was comparable with that reported by Fadaei *et al.* (2018), namely 22.49 d at the same temperature (25 °C) but on different prey, *T. urticae*. Other researchers have reported a great deal of variation in the longevity of *A. swirskii*. At 25 °C, Riahi *et al.* (2017a) reported longevity of 34.2 d on *T. urticae*; Bazgir *et al.* (2018) discovered longevity of 39.81 and 32.41 d on *E. frosti* and *C. irani*, respectively, whereas Hosseini *et al.* (2020) reported longevity of 25.21 d, 21.46 d, and 14.87 d on *T. urticae*, *C. lactis*, and *T. vaporariorum*, respectively. Considering previous works, *A. swirskii* longevity was moderate on *T. turkestanii* immatures.

In conclusion, this study provides baseline knowledge on the association between *A. swirskii* and *T. turkestanii*. The existing evidence proposes that *A. swirskii* can play an important role in reducing *T. turkestanii* populations. However, results of the functional response experiment indicate that *A. swirskii* could be more effective at low *T. turkestanii* population density. Nevertheless, it is necessary to consider the results with caution because these experiments have been conducted under simplified conditions using small arenas and no plant leaf substrates. In a whole plant system, *A. swirskii* adults can spread from one plant to the next and interact with other prey and predator populations, which could significantly affect its efficiency. Future research on prey stage preferences of *A. swirskii* and intraguild predation should add to the understanding of the capacity of *A. swirskii* as an effective biological control agent of *T. turkestanii*. Moreover, glasshouse (greenhouse) and field studies are necessary to determine the effectiveness of *A. swirskii* against *T. turkestanii* under more realistic conditions.

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