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reproduction in any medium, provided the original author and source are credited.
Functional response of the predatory mite *Amblyseius swirskii* (Acari: Phytoseiidae) to *Eotetranychus frosti* (Tetranychidae) and *Cenopalpus irani* (Tenuipalpidae)

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Original research

**ABSTRACT**

*Eotetranychus frosti* and *Cenopalpus irani* Dosse are pests of apple trees that are widely distributed in apple orchards in Iran. The functional responses and predation rates of *Amblyseius swirskii*, one of the most commonly utilized phytoseiid mites for biological control, on these two pests were evaluated at 25 ± 1 °C, with 16:8 h L: D, and a relative humidity of 60 ± 10 % on apple leaves. The results of predation rate experiments on the two prey species indicated that the predator consumed significantly more eggs than larvae and protonymphs whereas consumption of deutonymphs were very rare. Likewise, the results of logistic regression analysis showed that *A. swirskii* exhibited a Type II functional response on all immature stages of *E. frosti* and *C. irani*. Handling time (*T_\text{h}* \( )\) increased as prey size enlarged; the lowest handling times were determined as 0.4858 and 0.3819 h on eggs of *E. frosti* and *C. irani*, respectively, whereas the highest were found to be 1.4007 and 1.0190 h on deutonymphs, respectively. *Amblyseius swirskii* had the higher attack rate coefficient (*a* \( )\) on immature stages of *C. irani* than *E. frosti*. Attack rate coefficients (*a*) varied significantly between life stages of both pests with the highest attack rate obtained on eggs, followed by larvae, protonymphs, and deutonymphs. Results of this study suggest that *A. swirskii* could be a highly efficient biological control agent of *E. frosti* and *C. irani* at least at low prey densities.

**Keywords** apple; attack rate; biological control; handling time; predation rate

**Introduction**

*Eotetranychus frosti* (McGregor) (Acari: Tetranychidae) and *Cenopalpus irani* Dosse (Acari: Tenuipalpidae) are phytophagous mites that were reported on various plant species, especially Rosaceae in Western regions of Iran (Kamali \textit{et al.}, 2001; Mehrnejad, 2001; Khanjani \textit{et al.}, 2012). Occasional outbreaks of these pests have caused serious concerns about their detrimental effects on different plants (Darbemamieh, 2008; Khodayari \textit{et al.}, 2010; Bazgir \textit{et al.}, 2015a; Bazgir \textit{et al.}, 2015b). The population of these pests may reach high densities during the summer and cause significant damages to apple trees (Jafari and Bazgir, 2015). The feeding of both adults and immatures of these pests may result in significant plant damage such as low fruit quality, low plant vigor, defoliation, and significant losses in apple yield in the following season (Jafari \textit{et al.}, 2014).

The use of predatory mites of the family Phytoseiidae (Acari: Mesostigmata) is a reliable strategy to minimize pesticide usage, reducing environmental pollution, and protecting beneficial insect and mite species (Badii \textit{et al.}, 2004; Patel and Zhang, 2017). The predatory
mite *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) is one of the most efficient biological control agents of mites of several families such as Eriophyidae, Tenuipalpidae, and Tetranychidae and insect pests such as thrips and whiteflies (Buitenhuis et al., 2015; Calvo et al., 2015).

It has been commercially used in various countries around the world as a biological control agent (Arthurs et al., 2009; Park et al., 2011; Calvo et al., 2015; Fathipour et al., 2017b; Knapp et al., 2017). The development and reproduction capacity of this species on various kinds of pollen before the appearance of pests on the plant (Calvo et al., 2015; Fathipour et al., 2017b; Riahi et al., 2017a) and also its ability to control several pests simultaneously (Buitenhuis et al., 2015; Janssen and Sabelis, 2015) are important factors of this predator’s success in biological control programs.

The investigation of functional response characteristics of natural enemies is one of the crucial methods to evaluate their effective role in regulating pest populations (Fantinou et al., 2012). Among the functional response types reported by Holling (1959), predators with type III functional response are usually regarded as efficient in regulating prey populations; while natural enemies with type II functional response have been successfully used as biological control agents and have considerably gained the researchers’ attention (Xiao and Fadamiro, 2010; Ali et al., 2011; Carrillo and Pena, 2012; Ganjisaffar and Perring, 2015; Fathipour et al., 2017a,b; Fathipour et al., 2019). The functional response type and the value of its parameters may be affected by various factors such as prey species, prey stage, age of predator, the characteristics of host plant, temperature and humidity (Escudero and Ferragut, 2005; Ahn et al., 2010; Farazmand et al., 2012; Doker et al., 2016; Song et al., 2016; Fathipour et al., 2017a,b).

Though exploring the functional responses of *A. swirskii* feeding on *Tetranychus urticae* Koch has gained noticeable attention over recently (Xiao et al., 2013; Fathipour et al., 2017b; Fathipour et al., 2019), no information is available about its predator–prey interactions with other tetranychid and tenuipalpid mites.

In an earlier study, it was shown that *A. swirskii* has a high capacity of development and population growth when fed on the two pest species; *E. frosti* and *C. irani* (Bazgir et al., 2018). A critical step in determining the ability of *A. swirskii* to regulate *E. frosti* and *C. irani* is to assess its functional response and consumption rate when offered these preys. The objectives of this study were to determine the functional response type and parameters and feeding capacity of the predatory mite *A. swirskii* for varying densities of life stages of *E. frosti* and *C. irani*.

**Material and methods**

**Stock cultures of prey and predator**

*Eotetranychus frosti* and *C. irani* were collected from apple orchards in Chaghalvandi region in the vicinity of Khorraramabad, Lorestan province, southwestern Iran, and reared on apple leaf discs at 25 ± 1 °C, 60 ± 10 % RH and 16:8 h (L: D) photoperiod.

Initial populations of *A. swirskii* were obtained from Koppert Biological Systems, the Netherlands. The predatory mites were extracted from the bran carrier material and transferred to the leaf disks with a fine paintbrush. The predator was reared on apple leaves infested with mixed stages of each prey separately under the aforementioned laboratory conditions before the experiments, for several generations.

**Functional response experiments**

Experimental arenas consisted of a piece of apple leaf (4 cm in diameter) placed upside down on a wet cotton layer in a Petri dish (6 cm diameter) with a 0.5 cm hole drilled in its center. This Petri dish was placed in the middle of a larger Petri dish (9 cm) containing water to keep the leaves fresh. To prevent escaping predator and prey, a water-saturated cotton strip was placed
around the leaf margin. Before each test, 4-day old mated females of the predator were placed individually in experimental arenas and starved for 24 hours. To determine the functional response of the predator on each of the prey species (E. frosti and C. irani), a 24 h starved female predator was exposed to seven densities (2, 4, 8, 16, 32, 64 and 128 newly-emerged individuals) of different prey stages (egg, larvae, protonymph, and deutonymph). The prey mites were transferred onto leaf discs with a fine paintbrush (number 0000). After 24 h, the predators were removed and the number of prey individuals eaten was recorded by counting intact eggs and the carcasses of dead larvae, protonymphs or deutonymphs. Sixteen replicates were prepared for each prey density. All experiments were conducted in the laboratory at constant temperature 25 ± 1 °C, 60 ± 10 % RH and 16:8 h L: D photoperiod in an incubator.

Data analysis

The data on functional response were analyzed in two steps (Juliano, 2001). First, the logistic regression of the proportion of prey consumed as a function of initial density was used to determine the shape of the functional response curve of A. swirskii to different stages of E. frosti and C. irani:

\[
\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}{1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}
\]

where \(N_e\) is the number of prey consumed, \(N_0\) is the initial prey density, \((N_e/N_0)\) is the probability of prey consumption, and \(P_0, P_1, P_2\) and \(P_3\) are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated using the maximum likelihood method.

The type of functional response was determined by the signs of \(P_1\) and \(P_2\). If the linear coefficient is negative (\(P_1 < 0\)), it describes a type II functional response because the proportion of prey consumed declines monotonically with the initial prey density (Juliano, 2001).

In the next step, the handling time (\(T_h\)) and the attack rate (\(\alpha\)) coefficients of a type II response were estimated using the Rogers’ random predator equation (Rogers, 1972):

\[
N_e = N_0[1 - \exp(\alpha(T_hN_e - T))]
\]

where \(N_e\) is the number of prey consumed, \(N_0\) is the initial prey density, \(T\) is the searching time (1 day), \(\alpha\) is the 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).

The data on prey consumption was evaluated by three factors: the effect of prey species with two levels, prey stage with four levels and prey density with seven levels using 2^3 factorial analysis by SAS v.9.1 software (SAS Institute 2003). Differences between treatments were compared by Tukey’s test (\(\alpha = 0.05\)).

Results

Results of the logistic regression analysis showed significantly negative linear coefficient (\(P_1 < 0\)) and positive quadratic coefficient (\(P_2 > 0\)) for all prey stages, indicating that the percentage of prey consumed for each prey stage declined as prey density increased (Table 1). Thus, the predator, A. swirskii showed a type II functional response on all immature stages of both E. frosti and C. irani (Figure 1).

Amblyseius swirskii had a higher attack rate coefficient (\(\alpha\)) on immature stages of C. irani than E. frosti. The attack rate (\(\alpha\)) was the highest for predators feeding on eggs and estimated to be 0.1142 and 0.1404 h\(^{-1}\) on E. frosti and C. irani, respectively. The value of handling time (\(T_h\)) of A. swirskii was much shorter on immature stages of C. irani than E. frosti. The shortest handling time on both species was recorded for eggs (0.4858 and 0.3819 h on E. frosti and C. irani, respectively), followed by larvae, protonymphs and deutonymphs, respectively (Table 2).
Figure 1 Functional response curves of adult female *Amblyseius swirskii* to different stages of *Eotetranychus frosti* and *Cenopalpus irani*. Dots represent the observed numbers of prey consumed at each initial prey density, and lines were predicted by the random predator equation (Rogers, 1972).
Table 1 Maximum likelihood estimates from logistic regression of the proportion of both prey species *Eotetranychus frosti* and *Cenopalpus irani* consumed as a function of initial prey densities by adult female of *Amblyseius swirskii*.

<table>
<thead>
<tr>
<th>Prey Stage</th>
<th>Parameters</th>
<th>Estimate ± SE</th>
<th>$\chi^2$</th>
<th>P-value</th>
<th>Estimate ± SE</th>
<th>$\chi^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>Intercept (P₀)</td>
<td>3.8814 ± 0.4092</td>
<td>89.96</td>
<td>&lt;0.0001</td>
<td>2.8470 ± 0.3339</td>
<td>72.69</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Linear (P₁)</td>
<td>-0.1286 ± 0.0264</td>
<td>23.67</td>
<td>&lt;0.0001</td>
<td>-0.0572 ± 0.0233</td>
<td>6.04</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>Quadratic (P₂)</td>
<td>0.0015 ± 0.0005</td>
<td>10.37</td>
<td>0.0013</td>
<td>0.0005 ± 0.0004</td>
<td>1.59</td>
<td>0.2078</td>
</tr>
<tr>
<td></td>
<td>Cubic (P₃)</td>
<td>-5.93×10⁻⁶ ± 2.19×10⁻⁶</td>
<td>7.36</td>
<td>0.0067</td>
<td>-2.2×10⁻⁶ ± 2.04×10⁻⁶</td>
<td>1.16</td>
<td>0.2814</td>
</tr>
<tr>
<td>Larva</td>
<td>Intercept (P₀)</td>
<td>2.0679 ± 0.2442</td>
<td>71.71</td>
<td>&lt;0.0001</td>
<td>3.2964 ± 0.3488</td>
<td>89.33</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Linear (P₁)</td>
<td>-0.0700 ± 0.0176</td>
<td>15.89</td>
<td>&lt;0.0001</td>
<td>-0.1024 ± 0.0232</td>
<td>19.43</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic (P₂)</td>
<td>0.0007 ± 0.0003</td>
<td>4.57</td>
<td>0.0325</td>
<td>0.0011 ± 0.0004</td>
<td>6.82</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Cubic (P₃)</td>
<td>-2.67×10⁻⁶ ± 1.59×10⁻⁶</td>
<td>2.84</td>
<td>0.0922</td>
<td>-4.12×10⁻⁶ ± 1.98×10⁻⁶</td>
<td>4.35</td>
<td>0.0369</td>
</tr>
<tr>
<td>Protonymph</td>
<td>Intercept (P₀)</td>
<td>2.6324 ± 0.2658</td>
<td>98.08</td>
<td>&lt;0.0001</td>
<td>3.1658 ± 0.3279</td>
<td>93.21</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Linear (P₁)</td>
<td>-0.1183 ± 0.0186</td>
<td>40.38</td>
<td>&lt;0.0001</td>
<td>-0.1058 ± 0.0220</td>
<td>23.17</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic (P₂)</td>
<td>0.0015 ± 0.0003</td>
<td>18.78</td>
<td>&lt;0.0001</td>
<td>0.0001 ± 0.0004</td>
<td>7.99</td>
<td>0.0047</td>
</tr>
<tr>
<td></td>
<td>Cubic (P₃)</td>
<td>-6.18×10⁻⁷ ± 1.65×10⁻⁷</td>
<td>14.02</td>
<td>0.0002</td>
<td>-4.2×10⁻⁶ ± 1.88×10⁻⁶</td>
<td>4.98</td>
<td>0.0256</td>
</tr>
<tr>
<td>Deutonymph</td>
<td>Intercept (P₀)</td>
<td>0.0319 ± 0.1896</td>
<td>0.03</td>
<td>0.8664</td>
<td>0.9275 ± 0.1934</td>
<td>23</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Linear (P₁)</td>
<td>-0.0421 ± 0.0154</td>
<td>7.48</td>
<td>0.0062</td>
<td>-0.0807 ± 0.0153</td>
<td>27.82</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Quadratic (P₂)</td>
<td>0.0004 ± 0.0003</td>
<td>1.75</td>
<td>0.1861</td>
<td>0.0001 ± 0.0003</td>
<td>13.35</td>
<td>0.0003</td>
</tr>
<tr>
<td></td>
<td>Cubic (P₃)</td>
<td>-1.56×10⁻⁷ ± 1.52×10⁻⁷</td>
<td>1.05</td>
<td>0.3045</td>
<td>-4.78×10⁻⁶ ± 1.48×10⁻⁶</td>
<td>10.52</td>
<td>0.0012</td>
</tr>
</tbody>
</table>

The interaction between prey species and density was significant for the number of prey eaten ($F = 26.19; df = 6; P < 0.001$). The consumption rate of both prey species gradually increased with an increase in prey density. Nearly 90% of eggs, larvae, and protonymphs of *C. irani* and about 70% of the same stages of *E. frosti* were consumed at the lowest densities (2, 4, 8, and 16). Then, proportion of prey consumption for each prey stage by *A. swirskii* females decreased with increasing prey density (Figure 1).

The interaction between prey stage and different densities of prey was significant ($F = 73.51; df = 18; P < 0.001$). With increasing density of prey, the consumption rate was highest on eggs followed by larvae and protonymphs whereas the consumption rate of deutonymphs was lowest (Table 3). When each stage of two prey was offered to the predator, the interaction between prey species and prey stage was not significant ($F = 0.75; df = 3; P = 0.525$).

There was a significant effect of species ($F = 149.51; df = 1; P < 0.001$) on the number of prey consumed. *Amblyseius swirskii* attacked more *C. irani* than *E. frosti*. There was also a significant difference between the different prey densities ($F = 1711.70; df = 6; P < 0.001$) and between the life stages ($F = 519.63; df = 3; P < 0.001$) of the number of prey eaten. Average prey consumption at each density decreased with increasing size of the life stage. For example, the lowest mean number of prey consumed, at the density of 128, was estimated to be 14.1 and 19.2 prey/day for deutonymphs of *E. frosti* and *C. irani*, respectively (Table 3).

**Discussion**

In general, the predator’s consumption rate is inversely related to the size of life stage (Ali et al., 2011). In this study, the consumption rate of *A. swirskii* on eggs of *E. frosti* and *C. irani* was the highest, followed by the larvae and protonymphs, and the consumption rate of deutonymphs was the lowest. Soleymani et al. (2016) also reported higher consumption rates on eggs compared to other stages for *A. swirskii* feeding on *T. urticae*. The higher consumption
Table 2  Mean ± SE of attack rate and handling time for *Amblyseius swirskii* on different life stages of *Eotetranychus frosti* and *Cenopalpus irani*.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Stage</th>
<th>$\alpha$ (h$^{-1}$)</th>
<th>$T_h$ (h)</th>
<th>$T/T_h$(Prey/ day)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. frosti</em></td>
<td>Egg</td>
<td>0.1142 ± 0.0132</td>
<td>0.4858 ± 0.0186</td>
<td>49.4</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>(0.0880-0.1403)</td>
<td>(0.4489-0.5227)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Larva</td>
<td>0.0882 ± 0.0091</td>
<td>0.6533 ± 0.0233</td>
<td>36.74</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>(0.0701-0.1063)</td>
<td>(0.6072-0.6994)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protonymph</td>
<td>0.0874 ± 0.0103</td>
<td>0.8052 ± 0.0297</td>
<td>29.81</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>(0.0670-0.1078)</td>
<td>(0.7463-0.8640)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Deutonymph</td>
<td>0.0291 ± 0.0040</td>
<td>1.4007 ± 0.0907</td>
<td>17.13</td>
<td>0.91</td>
</tr>
<tr>
<td></td>
<td>(0.0212-0.0371)</td>
<td>(1.2209-1.5805)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. irani</em></td>
<td>Egg</td>
<td>0.1404 ± 0.0172</td>
<td>0.3819 ± 0.0151</td>
<td>62.84</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>(0.1064-0.1744)</td>
<td>(0.3520-0.4118)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Larva</td>
<td>0.1129 ± 0.0111</td>
<td>0.5262 ± 0.0166</td>
<td>45.61</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>(0.0908-0.1349)</td>
<td>(0.4933-0.5591)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protonymph</td>
<td>0.1186 ± 0.0143</td>
<td>0.6421 ± 0.0215</td>
<td>37.38</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>(0.0903-0.1470)</td>
<td>(0.5994-0.6848)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Deutonymph</td>
<td>0.0368 ± 0.0042</td>
<td>1.0190 ± 0.0567</td>
<td>23.55</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td>(0.0285-0.0452)</td>
<td>(0.9067-1.1313)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The values in parentheses represent 95% confidence intervals. $\alpha$, attack rate; $T_h$, handling time; $T/T_h$, maximum attack rate; $R^2$, coefficient of determination.

Rate on eggs compared to the other stages might be due to the fact that the weight of eggs is lower than other stages and thus predators need to feed on a greater number of eggs to get the same amount of nutrients (Ganjisaffar and Perring, 2015).

On the other hand, the mouthparts of *A. swirskii* may be better adapted to penetrate the egg chorion than the sclerotized cuticle of other stages. Usually, the predator successfully penetrated the egg chorion in a single attack attempt. But for feeding on nymphs and adults, the predator often required several attack attempts to penetrate the sclerotized cuticle of the mite, consequently a longer handling time on these stages was recorded (Carrillo and Pena, 2012; Ganjisaffar and Perring, 2015).

*Amblyseius swirskii* exhibited a type II functional response on all life stages of *E. frosti* and *C. irani*. The proportions of prey consumed by *A. swirskii* were higher at lower densities for all stages of *E. frosti* and *C. irani*. The proportion of killed prey decreased at high population densities likely due to satiation or interference on their predation capacity related to prey density (Carrillo and Pena, 2012). This pattern suggests that this predator could be more efficient at low or moderate densities of *E. frosti* and *C. irani*.

Our results are in line with Xiao et al. (2013) who reported that *A. swirskii* showed Type II functional response to *T. urticae* eggs. However, Fathipour et al. (2019) reported that the functional response of this predator fed on *T. urticae* eggs and nymphs changed to a Type III response when pollen was added as additional food source to the experimental arenas.

The Type II functional response is common in many phytoseiid species, including *Phytoseiulus persimilis* Athias-Henriot (Skirvin and Fenlon, 2003), *Euseius hibisci* (Chant) (Badii et al., 2004), *Neoseiulus californicus* (McGregor) (Xiao and Fadamiro, 2010; Farazmand...
Table 3 Mean ± SE daily consumption of *Amblyseius swirskii* at different densities of different stages of *Eotetranychus frosti* and *Cenopalpus irani*.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Prey density</th>
<th>Egg</th>
<th>Larva</th>
<th>Protonymph</th>
<th>Deutonymph</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. frosti</em></td>
<td>2</td>
<td>1.8 ± 0.14 f A</td>
<td>1.6 ± 0.13 f AB</td>
<td>1.7 ± 0.18 e AB</td>
<td>1.2 ± 0.19 c B</td>
</tr>
<tr>
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<td>3.8 ± 0.14 ef A</td>
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<td>3.7 ± 0.15 e A</td>
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<td>2.9 ± 0.28 c B</td>
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<td>11.6 ± 0.52 c B</td>
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<tr>
<td><em>C. irani</em></td>
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<td>1.8 ± 0.11 f A</td>
<td>1.8 ± 0.10 f A</td>
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<td>39.5 ± 1.21 a B</td>
<td>33.5 ± 1.48 a C</td>
<td>19.2 ± 0.96 a D</td>
</tr>
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</table>

The means followed by different small letters in the same column are significantly different within same prey species (*P* < 0.05, Tukey’s test)

The means followed by different capital letters in the same row are significantly different (*P* < 0.05, Tukey’s test)

Tetranychid mites have been utilized as prey in most of these studies; in contrast, the functional response of phytoseiid mites preying on tenuipalpid mites has been investigated in very few studies. Carrillo and Pena (2012) studied the functional response of *Amblyseius largoensis* (Muma) on *Raoiella indica* Hirst (Acari: Tenuipalpidae) and found a type II functional response. This type of response has also been observed in two other phytoseiid species namely, *Euseius mesembrinus* (Dean) and *Amblyseius herbicola*us (Chant), when feeding on *Brevipalpus californicus* (Banks) and *Brevipalpus phoenicis* (Geijskes), respectively (Badii et al., 1993; Reis et al., 2007). Although phytoseiid mites usually exhibit a type II functional response to their prey, this may change depending on physical characteristics of host plant (Skirvin and Fenlon, 2003), prey stage (Ganjisaffar and Perring, 2015), and different prey species (Escudero and Ferragut, 2005).

Two parameters that help to determine the magnitude of functional responses are the attack rate and the handling time (Pervez and Omkar, 2006). As an important indicator of the consumption rate and the predator efficiency, the handling time reflects the cumulative time needed for capturing, killing, and digesting the prey (Veeravel and Baskaran, 1997). Different factors can impinge on handling time such as the speed of the predator, movement of prey, and the time spent subduing individual prey (Hassell, 1978), which could be related to behavioral and structural prey defense mechanisms (Ali et al., 2011).

In our study, *A. swirskii* had a shorter handling time (*T_h*) on eggs than other stages. This value was lower when compared to *A. swirskii* feeding on eggs of *T. urticae* (Xiao et al., 2013; Fathipour et al., 2019); suggesting that this predator had a much stronger predation response on *E. frosti* and *C. irani*. Ganjisaffar and Perring (2015) reported that *G. flumenis* had a lower...
handling time on eggs than on other stages when consuming *Oligonychus pratensis* Banks. Attack rate coefficients ($\alpha$) varied between life stages of both pest species (*E. frosti* and *C. irani*) and in general reduced as prey size increased. This can be attributed to the immobility of eggs and their incapacity to defend themselves. The attack rate on the deutonymph stage was much lower than on the other stages; these findings concurred with reports for *G. flumenis* (Ganjisaffar and Perring, 2015), *N. womersleyi* (Ali et al., 2011), and *K. aberrans* (Kasap and Atlihan, 2011).

In our previous study, life history and predation parameters demonstrated that *A. swirskii* is able to feed and complete its development on *E. frosti* and *C. irani*; likewise, this predator can exhibit a high potential for population increase when fed on both pest mites (Bazgir et al., 2018). Results of the present study confirmed this. Also, higher proportions of prey were consumed by *A. swirskii* at lower densities of all stages of *E. frosti* and *C. irani*, suggesting a high searching ability of *A. swirskii*, and implying that this predator could be more efficient at regulating low densities of all stages of these pests.

Although functional response studies in laboratory condition provide some insight into the predator-prey interaction, this has been criticized for ignoring the environmental complexities and multispecies prey and predator systems that occur in the field (Ganjisaffar and Perring, 2015). For example, no or very little spider mite webbing was produced in laboratory experiments, however, in the field all stages of prey are surrounded by webbing which maybe a limiting factor of predation efficiency. Thus, field studies are required to determine the efficiency of *A. swirskii* and the improvement of management tactics for the control of *E. frosti* and *C. irani* under more realistic conditions.

### Acknowledgments

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### References


