Functional response and consumption rate of *Orius laevigatus* (Hemiptera: Anthocoridae) feeding on the melon aphid *Aphis gossypii* (Hemiptera: Aphididae) at three different temperatures

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Abstract: In this study, the effect of three temperatures was investigated on the functional response of *Orius laevigatus* to *Aphis gossypii* in climatic chambers at 20, 25, and 30 ± 1 °C, 60 ± 5% RH, and 16:8 h photoperiod. Different densities of first and second instar nymphs of *A. gossypii* (2, 4, 8, 16, 32, and 64) on cucumber leaf discs (6 cm in diameter) were separately offered to male and female predators. After 24 h, the number of consumed preys was recorded. Ten replicates per each aphid density were used. Based on the results, predator male and female exhibited types II, III, II and III, II, III functional responses at 20, 25 and 30 °C, respectively. Handling times (*T*ₗ) for males were 0.7798, 0.9177 and 0.4476 h and for females were 0.6874, 0.3921 and 0.2831 h at 20, 25 and 30 °C, respectively. Using the indicator variable method, pairwise comparisons of handling times of both males and females were significantly different. The theoretical maximum predation rate (*T*/*T*ₗ) of both males and females were obtained at 30 °C. The results revealed that *O. laevigatus* is more likely to be an effective biocontrol agent of *A. gossypii* at higher temperatures around 30 °C. However, additional studies under natural conditions are needed to provide further details of the predator-prey interactions.

Keywords: Predatory bug, melon aphid, cucumber, predator-prey interaction, temperature

Introduction

Cucumber plants in both open fields and greenhouses are attacked by various sucking pests (Rajabpour *et al*., 2011). The melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) is the most important one, which is widely distributed in tropical, subtropical and temperate regions (Satar *et al*., 1999). In Iran, this pest occurs in different regions especially north and south of the country (Taghizadeh Afshari *et al*., 2009). The adults and nymphs of *A. gossypii* settle on the underside of cucumber leaves or the growing tips of shoots and suck phloem sap from the host plant. Infested plants usually experience severe yield loss due to direct and indirect damages. Foliar chlorosis and leaf curling are the results of direct damage, which may hinder the efficient photosynthetic ability of plants (Blackman and Eastop, 2000). Moreover, the aphids transmit several viruses such as cucumber mosaic virus (CMV), resulting in indirect damage of the infested plants (Escriu *et al*., 2000). Pesticides are generally used to control *A. gossypii* on the...
crop. However, aphids develop resistance to commercial insecticides (Wang et al., 2002). Therefore, biological control seems a promising alternative to the use of insecticides (Karami et al., 2018).

The predatory bug Orius laevigatus Fieber (Hemiptera: Anthocoridae) is an important biological control agent in some regions of Iran such as Fars and Khorasan (Ghahari et al., 2009), the nymphs and adults of which can feed on a wide range of insect pests, such as Bemisia tabaci (Gennadius), Thrips tabaci (Lindeman), Frankliniella occidentalis (Pergande), Tetranychus urticae Koch, and A. gossypii (Venzon et al., 2002; Perdikis et al., 2008; Hosseini et al., 2010). Moreover, the predator can feed on pollen as an alternative diet (Cocuzza et al., 1997b). Mass introduction of O. laevigatus can usually provide adequate control of pests in cucumber greenhouses (Rajabpour et al., 2011).

The functional response is one of the important methods for evaluating the efficiency of a predator against a prey (Wiedemann and Smith, 1997). It refers to changes in the number of prey consumed by a predator per unit time in relation to initial prey density (Solomon, 1949), and it shows whether a predator is capable to regulate the density of its prey or not (Jervis and Kidd, 1996). Holling (1961) proposed three general types of functional response curves including type I, II, and III. Among these three types of functional response, types II and III have received the most attention (Fathipour et al., 2017). Functional response of natural enemies is influenced by both biotic (De Clercq et al., 2000, Hassanpour et al., 2011, Mottaghinia et al., 2015) and abiotic factors (Li et al., 2007, Jafari et al., 2012).

Insects are poikilotherms, so one important feature of insects’ life is their behavioral adaptation to the ubiquitous, seasonally changing environment (Tommasini and van Lenteren, 2003). Obviously, temperature has an important role in development and activities of Orius species and may be used for their mass production in biological control program (Carvalho et al., 2005). Some studies have only investigated the effect of temperature on biological characteristics of O. laevigatus. For example, Alauzet et al. (1994) showed that the best development and reproduction rates of O. laevigatus occurred at the temperature of 20 to 30 °C. Similarly, Cocuzza et al. (1997a) reported that survival, fecundity, and prey consumption of O. laevigatus were high at the temperature of 25 °C. Montserrat et al. (2000) studied the functional response of four heteropteran predators including, Dicyphus tamaninii Wagner, Macroleurophus caliginosus Wagner, Orius majusculus (Reuter), and O. laevigatus on greenhouse whitefly and western flower thrips. However, no other study has investigated the effect of temperature on the functional response of O. laevigatus preying upon aphid species. The objective of this study was to evaluate the predatory capacity of O. laevigatus through the study of its functional response at three temperatures to provide information on the potential use of the predator in integrated pest management (IPM) programs of A. gossypii.

Materials and Methods

Plants and insects

Seeds of cucumber (Cucumis sativus cv. Zohal) were sown in 20-cm-diameter plastic pots containing a mixture of field soil and cattle manure (3: 1% by volume). Plants were reared in a greenhouse at 25 ± 3 °C, 60 ± 10% RH, 16L: 8D photoperiod, and irrigated as needed.

Aphis gossypii used in this experiment was originally collected from infested cucumber greenhouses in the suburb of Ardabil, Iran. Aphids were transferred on grown plants by a fine brush. Before initiating the experiments, the aphids were reared on plants for more than three generations.

Orius laevigatus was obtained from a commercial supplier (Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands). Adults and nymphs were fed on frozen eggs of Anagasta kuehniella Zeller (Lepidoptera: Pyralidae). They were also provided with pollen every 3 days. The pollen was collected from a maize field and dried at 50 °C for 24 hours in an oven to prevent mould growth in the rearing container. The predators were kept and reared in...
clear plastic cages (height 18 cm, and diameter 8 cm) with two holes (2 cm diameter) in the lid and container body, which was covered by fine-mesh net for ventilation. Fresh bean pods of *Phaseolus vulgaris* L. were offered daily to the predators as oviposition substrate and moisture source. In order to reduce levels of cannibalism by predators, folded paper strips were added to each cage. Bean pods with eggs were incubated for five days until egg hatching. After that, nymphs were kept and fed in above-mentioned conditions up to adult emergence. Prior to the experiment, *O. laevigatus* was reared on *A. gossypii* as food for one generation. All insect cultures were reared in a controlled environment room at 25 ± 2 °C, 50 ± 10% RH and L16: D8 h photoperiod.

**Experimental design**

The experimental units were Petri dishes (8 cm in diameter) with a 2-cm-diameter hole in the lid, which was covered by fine-mesh net for ventilation. In each Petri dish, one leaf disc (6 cm in diameter) was centered upside down on wet cotton. Experiments were carried out in a climatic chamber at three temperature regimes of 20, 25, and 30 ± 1 °C, 55 ± 5% RH and a 16L: 8D h photoperiod. These temperatures were chosen because an optimum development and reproduction rate of *O. laevigatus*, as reported by Alauzet et al. (1994), happens between 20 and 30 °C. The preliminary experiments indicated nearly 100% survival of prey in the absence of predator. Adults of *O. laevigatus* were used in the experiments, because they are the most voracious stage of the predator. Before starting the experiment, the adults were starved for 24 h. For obtaining the same-aged adults, first instar nymphs (< 24 h old) of the predator were reared singly in Petri dishes (6 cm diameter) until they reached the adult stage. Predation was assessed by introduction of a single adult of *O. laevigatus* to each Petri dish (6 cm diameter and with a screen-covered hole in the lid for ventilation), provided with six different densities (2, 4, 8, 16, 32, and 64) of *A. gossypii* nymphs (a mixture of first and second instar nymphs). Since the response of adult male and female predators to the same temperature may be different, so both sexes were tested. There were ten replicates per each aphid density, temperature and predator sex. To prevent insects from escaping, each Petri dish was sealed with parafilm around the edge. After 24 h, the predators were removed from experimental arenas and the number of killed aphids was recorded.

**Statistical analysis**

The type of functional response was determined by logistic regression analysis of the proportion of prey consumed (*Nc*) as a function of the initial prey density (*N0*) using the categorical modeling procedure (PROC CATMOD) of the Statistical Analysis System (SAS Institute, 2001) as follows (Trexler and Travis, 1993):

\[
\frac{N_c}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}
\]

where *P0*, *P1*, *P2*, and *P3* are the constant, linear, quadratic and cubic coefficients, respectively. If the linear coefficient (*P1*) is negative, a type II functional response is evident, while a positive linear coefficient (*P1*) indicates a type III functional response (Juliano, 2001).

A random predator equation (Royama, 1971; Rogers, 1972) was fitted to the results using nonlinear least square regression procedure (PROC NLIN; SAS Institute, 2001) to estimate attack rate (*a*) and handling time (*Th*) of the predator. For the type II and type III functional responses, the following models were used to fit the data:

\[
N_c = N_0 \{ 1 - \exp[\alpha(T_h N_c - T)] \}
\]

\[
N_c = N_0 \left[ 1 - \exp \left( \frac{(d + bN_0)(T_h N_c - T)}{I + cN_0} \right) \right]
\]

where *Nc* is the number of prey consumed, *N0* is the initial prey density, *a* is the attack rate, *T* is the handling time per prey, *Tc* is the total time available for the predator (*T* = 24 h in this experiment), and *b*, *c*, and *d* are constants.
In the case where the data revealed a type III functional response, the parameters \( c \) and \( d \) were not significantly different from 0, so a reduced type III model was used to fit the experimental data:

\[
N_e = N_0 \{1 - \exp[bN_0(T_hN_0 - T)]\}
\]

Using the indicator variable method (Juliano, 2001), pairwise comparisons of functional response parameters (in similar types) of males and females of \( O. \) laevigatus were performed as follows:

\[
N_e = N_0 \{1 - \exp[-(\alpha + D_a(j))(T - T_h + D_th(j))N_e]\}
\]

where \( j \) is an indicator variable that takes on 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 attack rate for one stage is \( a \), and that for another stage is \( a + D_a \). Testing for a significant difference in searching efficiencies between two stages is accomplished by testing the null hypothesis that \( D_a \) includes 0 or not (Juliano, 2001).

The data were subjected to the one-way analysis of variance (ANOVA) using SPSS ver. 16.0 (SPSS, 2007) statistical software. When differences among treatments were significant, comparison among means were conducted using Tukey’s test at \( P < 0.05 \).

**Results**

The mean number of aphid nymphs consumed by male predator at 30 °C increased significantly with increase in the number of preys offered (from 16 to 64 preys). Similar trend was observed for female predator at 25 and 30 °C. (Tables 1 and 2). At highest prey density, the highest numbers of prey consumed by both male and female predators were obtained at 30 °C.

The linear coefficient \( (P_1) \) of the logistic regression of \( O. \) laevigatus females at 25 °C, and those of males at 20 and 30 °C were negative, which indicated the type II functional response (Table 3). At these temperatures, the percentage of aphids consumed by both sexes of the predator declined as aphid density increased (Fig. 1).

**Table 1** Prey consumption by adult male of \( Orius \) laevigatus when feeding on various densities of \( Aphis \) gossypii at different temperatures.

<table>
<thead>
<tr>
<th>Prey density</th>
<th>Number of prey consumed (Mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 °C</td>
</tr>
<tr>
<td>2</td>
<td>1.6 ± 0.22Ac</td>
</tr>
<tr>
<td>4</td>
<td>3.5 ± 0.22Ac</td>
</tr>
<tr>
<td>8</td>
<td>6.6 ± 0.43Abc</td>
</tr>
<tr>
<td>16</td>
<td>12.2 ± 1.12Ab</td>
</tr>
<tr>
<td>32</td>
<td>19.3 ± 1.65Aa</td>
</tr>
<tr>
<td>64</td>
<td>24.5 ± 2.60Ba</td>
</tr>
</tbody>
</table>

Values followed by different lowercase letters in the same column and uppercase letters in the same row are significantly different (Tukey’s test, \( P < 0.05 \)).

**Table 2** Prey consumption by adult female of \( Orius \) laevigatus when feeding on various densities of \( Aphis \) gossypii at different temperatures.

<table>
<thead>
<tr>
<th>Prey density</th>
<th>Number of prey consumed (Mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 °C</td>
</tr>
<tr>
<td>2</td>
<td>1.6 ± 0.22Ac</td>
</tr>
<tr>
<td>4</td>
<td>2.7 ± 0.52Ac</td>
</tr>
<tr>
<td>8</td>
<td>5.7 ± 0.84Ac</td>
</tr>
<tr>
<td>16</td>
<td>14.2 ± 0.68Ab</td>
</tr>
<tr>
<td>32</td>
<td>18.9 ± 2.54Bb</td>
</tr>
<tr>
<td>64</td>
<td>32.9 ± 4.06Ba</td>
</tr>
</tbody>
</table>

Values followed by different lowercase letters in a same column and uppercase letters in a same row are significantly different (Tukey’s test, \( P < 0.05 \)).
Furthermore, the logistic regression analysis led to a positive value of $P_1$ for the females of *O. laevigatus* at 20 and 30 °C and for the males at 25 °C, which showed type III functional response (Table 3). At the mentioned temperatures, the percentage of the prey consumed by the predator at low prey densities was relatively low, then increased, and finally leveled off and decreased at a density over 16 and 32 aphids for males and females, respectively (Fig. 1).

The coefficients of attack rate and handling time were the parameters used to determine the magnitude of the functional response of *O. laevigatus* (Fathipour et al., 2017). At different temperatures, the predator responded differently to increasing aphid density. Handling time decreased as temperature increased for both males (except from 20 to 25 °C) and females. The shortest handling times were recorded at 30 °C for both males and females. However, the longest ones were at 20 and 25 °C for females and males, respectively (Table 4).

The results for the comparison of functional response parameters (attack rates (for the functional response type II; the males), and the parameter of $b$ (for the functional response type III; the females), and handling times) showed that the values estimated for $D_{Th}$ were significantly different from zero and the handling time of *O. laevigatus* decreased significantly when the temperature increased from 20 to 30 °C. However, the values estimated for $D_a$ as well as $D_b$ were not significantly different from zero. The handling times of both males and females estimated at 30 °C was considerably shorter than those at 20 °C (Table 5).

The theoretical maximum predation rate ($T/T_h$) of the females of *O. laevigatus* increased with increasing the temperature. For the males, the $T/T_h$ values ranged from 26.12 to 53.62 preys day$^{-1}$, the highest value of which was obtained at 30 °C (Table 4).

Table 3 Maximum likelihood estimates from logistic regressions of the proportion of *Aphis gossypii* nymphs preayed by *Orius laevigatus* as a function of initial prey density at different temperatures.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Temperature (°C)</th>
<th>Parameters$^1$</th>
<th>Estimate ± SE</th>
<th>$\chi^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>20</td>
<td>$P_0$</td>
<td>1.9953 ± 0.28100</td>
<td>50.43</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_1$</td>
<td>-0.0591 ± 0.01690</td>
<td>12.24</td>
<td>0.0005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_2$</td>
<td>0.00032 ± 0.00021</td>
<td>2.41</td>
<td>0.1209</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_3$</td>
<td>0.00008 ± 0.00003</td>
<td>7.12</td>
<td>0.0076</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>$P_0$</td>
<td>1.2764 ± 0.53720</td>
<td>5.65</td>
<td>0.0175</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_1$</td>
<td>0.1723 ± 0.08550</td>
<td>4.06</td>
<td>0.0438</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_2$</td>
<td>-0.0085 ± 0.00324</td>
<td>6.84</td>
<td>0.0089</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_3$</td>
<td>0.00008 ± 0.00003</td>
<td>7.12</td>
<td>0.0076</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>$P_0$</td>
<td>2.4772 ± 0.34480</td>
<td>51.61</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_1$</td>
<td>-0.0476 ± 0.02030</td>
<td>5.50</td>
<td>0.0191</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_2$</td>
<td>0.00024 ± 0.00020</td>
<td>1.00</td>
<td>0.3185</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_3$</td>
<td>0.00014 ± 0.00003</td>
<td>25.64</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Female</td>
<td>20</td>
<td>$P_0$</td>
<td>-0.2031 ± 0.42020</td>
<td>0.23</td>
<td>0.6289</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_1$</td>
<td>0.3124 ± 0.07070</td>
<td>19.51</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_2$</td>
<td>-0.0136 ± 0.00270</td>
<td>24.68</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_3$</td>
<td>0.00014 ± 0.00003</td>
<td>25.64</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>$P_0$</td>
<td>3.0231 ± 0.37990</td>
<td>63.31</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_1$</td>
<td>-0.0838 ± 0.02160</td>
<td>15.10</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_2$</td>
<td>0.00066 ± 0.00025</td>
<td>6.71</td>
<td>0.0096</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_3$</td>
<td>1.7818 ± 0.31150</td>
<td>32.71</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>$P_0$</td>
<td>0.0117 ± 0.02000</td>
<td>0.34</td>
<td>0.5579</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_1$</td>
<td>-0.00041 ± 0.00025</td>
<td>2.65</td>
<td>0.1034</td>
</tr>
</tbody>
</table>

$^1P_0$, $P_1$, $P_2$, and $P_3$ are the constant, linear, quadratic and cubic coefficients, respectively.
Figure 1 Functional response of females (left) and males (right) of Orius laevigatus on different densities of Aphis gossypii nymphs at three temperatures. The data points and solid lines represent the number of Aphis gossypii killed and the predictions of the models, respectively.

Table 4 Parameters of functional response of Orius laevigatus feeding on Aphis gossypii at different temperatures.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Temp. (°C)</th>
<th>Functional Response Type</th>
<th>α ± SE (95% CI)$^1$</th>
<th>$\alpha_0$ (± SE) (95% CI)$^2$</th>
<th>T/Th</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>20</td>
<td>II</td>
<td>0.1002 ± 0.0264 (0.0473 - 0.1531)</td>
<td>0.7798 ± 0.0869 (0.6058 - 0.9538)</td>
<td>26.12</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>III</td>
<td>0.0148 ± 0.0045 (0.0060 - 0.0237)</td>
<td>0.9177 ± 0.0384 (0.8420 - 0.9956)</td>
<td>25.62</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>II</td>
<td>0.1101 ± 0.0265 (0.0571 - 0.1632)</td>
<td>0.4476 ± 0.0655 (0.3165 - 0.5788)</td>
<td>34.91</td>
<td>0.66</td>
</tr>
<tr>
<td>Female</td>
<td>20</td>
<td>III</td>
<td>0.0047 ± 0.0014 (0.0018 - 0.0075)</td>
<td>0.6874 ± 0.0610 (0.5653 - 0.8094)</td>
<td>34.91</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>II</td>
<td>0.0955 ± 0.0234 (0.0486 - 0.1424)</td>
<td>0.3921 ± 0.0755 (0.2409 - 0.5430)</td>
<td>61.21</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>III</td>
<td>0.1092 ± 0.0266 (0.0560 - 0.1624)</td>
<td>0.2831 ± 0.0696 (0.1437 - 0.4225)</td>
<td>84.78</td>
<td>0.92</td>
</tr>
</tbody>
</table>

$^1$ CI: Confidence intervals, $\alpha$: attack rate. $^2$Th: handling time of the predator.
Table 5  The parameters estimated using combined equation for comparison of functional response parameters of Orius laevigatus males and females feeding on Aphis gossypii at two temperatures of 20 and 30 °C.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Temperature (°C)</th>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>Approximate 95% Confidence Limits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 - 30</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td></td>
<td>$D_a$</td>
<td>0.0086</td>
<td>0.0379</td>
<td>-0.0665 to 0.0837</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$D_{Th}$</td>
<td>-0.3352</td>
<td>0.1101</td>
<td>-0.5532 to -0.1172</td>
</tr>
<tr>
<td>Female</td>
<td>20 - 30</td>
<td>$D_a$</td>
<td>0.0418</td>
<td>0.0364</td>
<td>-0.0303 to 0.1140</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$D_{Th}$</td>
<td>-0.1309</td>
<td>0.1352</td>
<td>-0.3987 to -0.1369</td>
</tr>
</tbody>
</table>

Discussion

The results revealed that the mean number of A. gossypii nymphs killed by O. laevigatus males and females increased with an increase in prey density and temperature. The mean number of preys eaten by both males and females was 1.6 ± 0.22 at the density of 2 preys at 20 °C and reached a maximum of 36.5 ± 2.74 (for male) and 45.1 ± 3.16 (for female) from total number of 64 preys at 30 °C. Higher consumption rate of females may be associated with additional food requirements for egg production (Pakyari and Enkegaard, 2012).

In the present study, the type of functional response of O. laevigatus at different temperatures varied between type II and III for both adult males and females. Data provided a good fit to type II functional response model at 25 °C for the females of O. laevigatus and at 20 and 30 °C for the males. In this type of response, the predation rate decreases monotonically with increasing prey density. Furthermore, data from 20 and 30 °C for the females and 25 °C for the males of O. laevigatus fit a type III response in which predation rate increases at low prey densities, and then decreases at higher prey densities with a sigmoid curve that potentially regulates the prey population. Several factors including predator learning, prey switching as well as the availability of prey to refuge have been suggested to generate type III functional response (Holling, 1965; Messina and Hanks, 1998).

The type of functional response of a natural enemy may vary from one type to another as environmental conditions, especially temperature change (Thompson, 1978). According to McCaffrey and Horsburgh (1986), O. insidiousus showed either type II or III responses to densities of the European red mite, Panonychus ulmi Koch at different temperatures. Similarly, Hassanpour et al. (2015) reported that the functional responses of both male and female of O. laevigatus towards T. urticae were type II at 20 and 25 °C and type III at 30 °C.

Both type II and III functional responses have been reported for other Orius species. For example, the type of functional response of O. albidipennis Reuter to Megalurothrips sjostedti Tryborn (Gitonga et al., 2002), O. insidiousus (Say) to Aphis glycines Matsumura (Rutledge and O’Neil, 2005), O. albidipennis to T. tabaci and Aphis pomi De Geer (Lotfi et al., 2013), O. insidiousus to A. gossypii (Veiga et al., 2014), O. tristicolor (White) to Tuta absoluta (Meyrick) (Queiroz et al., 2015) was type II and the type of functional response of O. albidipennis (Reuter) to T. urticae, A. gossypii (Noruzi et al., 2014), and T. absoluta (Salehi et al., 2016) was type III.

In this study, the type of the functional response of O. laevigatus varied under different temperatures. The effect of temperature on both attack rate and handling time of predators has been previously reported by different researchers (e.g., Mohaghegh et al., 2001; Jafari et al., 2012; Ziaei Madbouni et al., 2017).

Based on the results, the parameter of b estimated for predator female (type III functional response) increased with increasing temperature from 20 to 30 °C, but the values of
the handling time decreased with increasing temperature. The same trend was observed for the handling time of *O. laevigatus* males with increasing temperature. Similarly, Ahn et al. (2010) reported that the handling time of the predatory mite, *Neoseiulus californicus* (McGregor) when attacking *T. urticae* decreased significantly with increasing temperature. This reveals that both males and females of *O. laevigatus* were more active at high temperatures and spent more time searching and feeding, whereas at low temperatures non-searching activities such as resting increased. The handling time is a good indicator of the consumption rate and predator efficacy, since it determines the cumulative effect of different components such as time taken during capturing, killing, subduing and digesting the prey by the predator (Veeravel and Baskaran, 1997). Therefore, significant variation in the handling time estimated for a predator on prey at different temperatures reveals that any one of the above-mentioned components of the handling time might have been affected by temperature. Also, in the present study, the highest handling time estimated for females at 20 °C might be as a result of an increase in non-searching activities such as resting.

The highest maximum predation rate ($T/T_h$) of males and females happened at 30 °C. These results show that both males and females of *O. laevigatus* are expected to be more efficient at 30 °C than at the two lower temperatures used in this study. However, females with their density-dependent predation can have the highest efficiency against *A. gossypii* at 30 °C. Hassanpour et al. (2015) reported that the maximum predation rates of both males and females of *O. laevigatus* to *T. urticae* occurred at 25 °C. These results confirm the influence of temperature and prey type in predation rate of predators.

In the present study, the temperature had a significant impact on functional response and predation of *O. laevigatus* to *A. gossypii*. It has been reported that *O. laevigatus* is well adapted to low temperatures (Cocuzza et al., 1997a), but the results of this study suggested that the optimum temperature for adults of *O. laevigatus* according to the highest value of predation rate and the lowest value of handling time was around 30 °C. Therefore, at high temperatures especially in greenhouses, *O. laevigatus* could forage and consume aphids at higher rates, which could be considered a good point for this predator, because previous studies showed that the optimum aphid development temperature is 25 to 30 °C (Kersting et al., 1999; Nimblett et al., 2010). In this study, only the females presented type III response at this temperature and seem more suitable for suppressing *A. gossypii* populations, but males with their type II response could be efficient in pest control, because many predators previously used as successful biological control agents showed the type II functional responses (De Clercq et al., 2000; van Lenteren et al., 2016). It is important to note that beside climatic conditions, some other factors such as habitat heterogeneity (Lipcius and Hines, 1986), competition (Pervez and Omkar, 2005), density and distribution of the prey (Yasuda and Ishikawa, 2001), and physical and biochemical characteristics of host plants (Rutledge and O’Neil, 2005) can affect the ability of predator to suppress prey population growth. Although the present study provided preliminary information on the efficacy of *O. laevigatus* on *A. gossypii*, the functional response is not the only criterion determining the failure or success of a biological control agent and additional data must be collected in the natural conditions. In addition, functional response experiments in small-scale setups (such as Petri dish) may have little resemblance of those measured in natural conditions. Therefore, supplementary studies under complex field conditions are needed to provide further details of the predator-prey interactions (O’Neil 1989).

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Statement of Conflicting Interests
The authors state that there is no conflict of interest.

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Authors’ Contributions
All authors have contributed significantly, and that all authors are in agreement with the content of the manuscript.

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واکنش تابعی و نرخ مصرف سن O. laevigatus (Hemiptera: Anthocoridae) در سه دمای مختلف Aphis gossypii (Hemiptera: Aphididae)

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چکیده: در این تحقیق، اثر دمای‌های مختلف روی واکنش تابعی سن شکارگر و نرخ مصرف سن O. laevigatus در ارتفاع نوری 16 ساعت روزانه و 8 ساعت تاریکی، مورد بررسی قرار گرفت. نتایج نشان داد که در دمای‌های متوسط (32 ± 4 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های بالاتر (34 و 36 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های پایین‌تر (30 و 28 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های پایین‌تر (30 و 28 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های پایین‌تر (30 و 28 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های پایین‌تر (30 و 28 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های پایین‌تر (30 و 28 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود. در دمای‌های پایین‌تر (30 و 28 درجه سانتی‌گراد) نرخ مصرف سن در این سنگینها از دمای‌های دیگر متفاوت بود.

واژگان کلیدی: سن شکارگر، شکارگر-شکارگر، سنگین، نرخ مصرف سن، O. laevigatus، Aphis gossypii