Aggressiveness and predation preference of predatory mites

Amblyseius swirskii (Athias-Henriot), Neoseiulus californicus (McGregor) and Phytoseiulus persimilis (Athias-Henriot) (Acari: Phytoseiidae) towards to heterospecific larvae

SOMAYEH HAGHANI, AZADEH ZAHEDI GOLPAYEGANI, ALIREZA SABOORI & HOSSEIN ALLAHRARI

Department of Plant protection, Faculty of Agriculture, University of Tehran, Karaj, Iran
E-mails: haghani.somayeh86@gmail.com, zahedig@ut.ac.ir, saboori@ut.ac.ir, allahyar@ut.ac.ir

*Corresponding author: E-mail: zahedig@ut.ac.ir

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Abstract
Behavioral characteristics such as aggressiveness and predation preference of the phytoseiid predatory species, Amblyseius swirskii, Neoseiulus californicus and Phytoseiulus persimilis (Acari: Phytoseiidae) were investigated when applied together. We quantified the chance and time of a successful attack to a heterospecific larva as aggressiveness of adult females. In order to determine the predation preference of adult females equal combination of con/heterospecific larvae were presented to as prey in absence of their main prey (Tetranychus urticae Koch) for 24 h. Experiments were carried out in growth chamber at 25±1 ºC, 65±5% RH and 16:8 (L: D) hour photoperiod regimens. The results showed that adult females of N. californicus needed 39.65±7.46 min. to attack and kill the larva of P. persimilis which was remarkably less than that recorded (227.80±28.38 min.) for adult females of P. persimilis to attack and kill N. californicus larva. N. californicus was estimated more aggressive than P. persimilis. The mean estimated attack time of A. swirskii and P. persimilis was estimated 18.55±2.89 and 201.70±25.42 min., respectively. A. swirskii was considered more aggressive than P. persimilis against heterospecific larvae. The predation preference index (Manly’s β) were indicated that N. californicus was able to recognize con/heterospecific larva, resulted more preference for heterospecific larvae (P. persimilis) in absence of T. urticae, while adult P. persimilis showed no preference (between con and heterospecific larva). Manly’s β, for A. swirskii was 0.706 and 0.294, for P. persimilis 0.369 and 0.630 on hetero and conspecific larvae, respectively. Results of this study showed that, A. swirskii and N. californicus are general predators were able to recognize con/heterospecific larva and preferred to feed on heterospecific larvae and get benefit from intraguild predation.

Key words: Intraguild predation, Phytoseiidae, cannibalism, prey preference.

Introduction
Cannibalism has been defined as the killing and consumption of conspecific individuals and it is considered as an important behavioral trait which affects the ecology and population dynamics of many taxa (Elgar & Crespi 1992; Schausberger 2003). The Cannibalism is expected to happen when the preferred-prey density is not enough (Polis 1981; Momen & Abdel-Khalek 2009). Intraguild predation, the predation among various life stages between different species within a guild (Momen & Abdel-Khalek 2009) happens when one...
species - being the intraguild predator - and the other - intraguild prey - share the same food (Polis et al. 1989). Both interactions are important factors in the biology and ecology of many species and have main effect on population structure and dynamics and species composition in the habitat (Fox 1975; Polis 1981; Rosenheim et al. 1995).

Many studies have demonstrated that cannibalism and intraguild predation are common among phytoseiid mites (Walzer & Schausberger 1999; Castagnoli et al. 2002; Momen & Abdel-Khalek 2009). Intraguild predation is mostly common in generalist species (Rosenheim et al. 1995; Momen & Abdel-Khalek 2009). Momen & Abdel-Khalek (2009) studied the intraguild predation and cannibalism on eggs and immatures by adult females of *Euseius scutalis* (Athias-Henriot), *Typhlodromips swirskii* (Athias-Henriot) and *Typhlodromus athiasae* Porath and Swirski are showed that the adult females of all three species exhibited higher predation rates on larvae that on protonymphs. They concluded that phytoseiid immatures were suitable prey for polyphagous phytoseiid predatory mites. Schausberger and Croft (1999, 2000) showed that cannibalism tendency varied among species and their life stage. Previous studies have revealed that while the cannibal stages were mostly limited to adult females the victim stages were mostly eggs and larvae in phytoseiid mites (Croft & McMurtry 1972; Croft et al. 1995; Croft & Croft 1996; Croft et al. 1996; Schausberger 1997; MacRae & Croft 1997; Monetti & Croft 1997; Schausberger & Croft 1999, 2000). There are also some studies reported that adult *T. pyri* Scheuten and all developmental stages of *N. fallacis* (Garman) could be consumed as prey (Croft et al. 1996). Schausberger & Croft (2000) noted that the phytoseiid cannibalism tendency could be reflected in their aggressiveness and predation rates. They reported that *E. finlandicus* (Oudemans), *N. cucumeris* (Oudemans) and *N. fallacis* were aggressive cannibals while *T. pyri* showed more patient behavior. Zhang & Croft (1994) demonstrated that as larva is a very vulnerable stage when confront with cannibals, it has a high tendency to escape from being consumed. They explained that this might be the reason why in some species, larva do not prey while in the others (*E. finlandicus*) are obligatory feeding.

According to Schausberger & Croft (2000) aggressiveness - the propensity of adult females to attack and kill con- and heterospecific larvae - could be measured as the survival time of larvae when caged singly with an adult female. They noted that aggressiveness of adult cannibal females showed only a slight difference among generalist and specialist predators. Among the life stages of phytoseiid mites, the adult female is usually preys most frequently on other life stages, and the larva is usually the life stage most often preyed upon by adult ones (Yao & Chant 1989; MacRae & Croft 1993; Croft et al. 1996, Schausberger 1997, 2003; Walzer & Schausberger 1999a, Schausberger & Croft, 2003; Abad-Moyano et al. 2010).

*N. californicus* (McGregor) as a control agent of tetranychid mites is one of the main phytoseiid predators that always is associated with spider mite dense webbing (Type II lifestyle) and has the ability of cutting the strands of web with their chelicerae (McMurtry et al. 2013). *N. californicus* is an efficient biocontrol agent with a broad diet recommended for the control of spider mites, thrips and tarsonemid mites (Rahman et al. 2009; McMurtry et al. 2013). It is considered to be more tolerant species to the low relative humidity levels compared with other phytoseiid mites that are currently used for biological control purpose, all over the world. Comparing with *P. persimilis* (Athias-Henriot), researchers have reported *N. californicus* to show higher adaptation to prey low densities (Toldi et al. 2013). The specialist predatory mite, *P. persimilis* (Type I lifestyle) has been well studied with respect to its ability to control spider mites in greenhouses (Maleknia et al. 2014). It is sensitive to higher levels of temperature and lower levels of humidity. *P. persimilis* has specially been used to control *T. urticae*. According to van Maanen et al. (2010) *A. swirskii* (Athias-Henriot) is considered as another effective generalist and polyphagous predatory mite, prey on many species such as gall mites (El-Laiithy 1998), spider mites (Swirski et al. 1967; El-Laiithy & Fouly 1992; Momen & El-Sawy 1993; van Houten et al. 2007a), tarsonemid mites (Tal et al. 2007), citrus rust mites (Argov et al. 2007), whiteflies (Swirski et al. 1967; Nomikou et al. 2001, 2002; Hoogerbrugge et al. 2005; Calvo et al. 2006), thrips (van Houten et al. 2005; Messelink et al. 2005, 2006; Wimmer et al. 2008) and pollen (Ragusa & Swirski 1975; Nomikou et al. 2003).

Specialist predators are adapted to exploit only one or a few prey types and are highly evolved in distinguishing and recognizing the preferred prey (Hislop & Prokopy 1981; Sabelis & Dicke 1985; Dicke et al. 1998).

Cannibalism and intraguild predation are common behaviors among phytoseiid mites (MacRae and Croft 1993; Zhang & Croft 1995a, b; Schausberger 1997, 1999a). They can be classified as generalists and specialists according to their diet types (McMurtry & Rodriguez 1987). Diet specialization is reflected in the predator trends to cannibalize on con-heterospecific individuals (Croft et al. 1996, 1998; McMurtry &
Croft 1997; Schausberger 1999b). Schausberger & Croft (1999) also emphasized that the cannibalism tendency depended only on predator and prey stages and not the diet specialization. Janssen et al. (1997) emphasized that P. persimilis avoided odors related to spider mite infested plants (in olfactory experiments) when conspecifics were present (as odor source), while this did not happen when conspecifics were replaced by N. californicus (as odor source). They reported this behavior in a reverse trend when P. persimilis was replaced by N. californicus as searching predator. We tested aggressiveness, i.e. the propensity to attack and kill another species larva (Abad-Moyano et al. 2010). This study was initiated to observe and describe the IG interactions among three phytoseiid species, A. swirskii, N. californicus and P. persimilis that are currently mass cultured and utilized all over the world. Furthermore, we assessed the predation preference of adult female (either of the species) when held with con- and heterospecific larvae without T. urticae.

Material and Methods

Plant source
The common bean plant, Phaseolus vulgaris L. (Fabaceae), was grown in plastic pots (top 5 cm diameter and 10 cm height) containing mixture of cocopeat and perlite (1:1). The potted plants were irrigated every day with tap water and a solution of NPK (20×20×20) fertilizer was periodically added, and kept in controlled conditions (25 ± 2 °C, 16L: 8D h photoperiod and 60±5 % RH) in growth chambers.

Prey source
The two-spotted spider mite, T. urticae was collected from the main stock culture reared on bean plants in laboratory of Acarology, Department of Plant Protection, College of Agriculture, University of Tehran, Karaj, Iran in July 2011. The prey rearing was continued on the same host plant at the same conditions as described for plant rearing in especial cages to keep plant free from mite infestations.

Predator source
Predatory mites A. swirskii, N. californicus and P. persimilis, were collected from the stock culture of laboratory of Acarology, Department of Plant Protection, College of Agriculture, University of Tehran, Karaj, Iran (main source: Koppert company). The predatory mites were reared on spider mite infested bean leaves in growth chambers (25±1 °C, 65±5% RH and 16:8 (L: D) hour photoperiod). The predator rearing unit included a piece of green hard plastic sheet on a water-saturated sponge in a plastic container (24×16×11 cm). The borders of sponge were surrounded with moistened tissue papers to ensure a constant water supply to the phytoseiids and prevent them from escaping (Overmeer 1985; Walzer & Schausberger 1999). T. urticae infested bean leaves were used to feed the predatory mites. For A. swirskii and N. californicus rearing unit some corn pollen was offered as supplementary food two times a week. To obtain the same-aged female predators for the experiments, the newly laid eggs were collected daily and transferred to the new arenas (the same as rearing unit as described above). Upon appearance of adult females of the predatory mites, they mated with males within 24 h. These females were used in the experiments.

Aggressiveness of adult females in intraduild predation on larvae
We quantified the chance and time of a successful attack that led to a heterospecific larva being killed as aggressiveness of adult females. IG couples tested were A. swirskii - P. persimilis, N. californicus - P. persimilis and vice versa. The experimental units consisted detached bean leaf squares (2.5 × 2.5 cm) placed upside down on a water-saturated cotton layer in a plastic Petri dish (9 cm diameter × 1.5 cm height) half filled with water. Wet tissue paper strips were placed around the leaf margin to prevent the mites from escaping. All experiments were performed under controlled conditions (the same as rearing unit as described above). Predatory mites were taken randomly from rearing units and starved for 24 h in 20 replicates for each test. We removed the laid eggs at the end of the starvation period. The heterospecific larva (either of the predator species) was added to the arena and its survival was checked every 5 min. for 7 hour period. We stopped monitoring when had been killed or remained survived till the end of the experiment (Abad-Moyano et al. 2010).
Predation preference of adult female when held with con- and heterospecific larvae without T. urticae

The predation preference of both phytoseiid species when were kept with con- and heterospecific phytoseiids were determined in order to experiment were carried out as follows:

Experiment 1: For both predators (N. californicus and P. persimilis), adult gravid females were taken randomly from rearing units and starved for 24 h. The experimental units consisted of leaf squares (2.5 ×2.5 cm) cut from fresh bean leaves placed upside down on a water-saturated cotton layer in a plastic Petri dish (9 cm diameter × 1.5 cm height) half filled with water. Wet tissue paper strips were placed around the leaf margin to prevent the mites from escaping. All experiments were performed under controlled conditions (same conditions described above). After 24 h starvation, each female was offered with 4 larvae each of con- and heterospecifics. Each predator was allowed to feed on the larvae for a total of 24 h. At the end of 24 h, the number of surviving larvae of phytoseiid was recorded. Each treatment had 20 replicates. The number of larvae for this experiment was determined on the basis of preliminary experiments.

Experiment 2: The same procedure was applied for A. swirskii and P. persimilis, predators.

Statistical analysis
Attacks by IG predator female were the only cause of larval mortality. Analysis of data was used with independent t-test and Mann-Whitney U-tests (non-parametric) in Sigma Plot 12. Predation preferences were quantified with the index β (Manly et al. 1972):

\[
\beta_1 = \frac{\log \left( \frac{e_1}{A_1} \right)}{\log \left( \frac{e_1}{A_1} \right) + \log \left( \frac{e_2}{A_2} \right)}
\]

Where \( \beta_1 \) is the preference to prey type 1, \( e_1 \) and \( e_2 \) are the number of prey type 1 and type 2 remaining after the experiment, \( A_1 \) and \( A_2 \) are the number of prey type 1 and type 2 presented to the predator. If the preference index is close to 1, the predator prefers prey type 1, and if close to 0 the prey type 2 is preferred. An index value close to 0.5 indicates no preference, i.e. predation is random (Cock 1978; Sherratt & Harvey 1993). The \( \beta \)–value was calculated for each replicate and averaged to determine the mean \( \beta \)–value for each treatment. Differences between treatments were analyzed by paired sample t-test and Mann-Whitney U-tests in Sigma Plot 12.

Results

Adult females of N. californicus needed on average 39.65±7.46 min. (mean±SE) to attack and kill the larvae of P. persimilis which was remarkably less than that recorded (227.80±28.38 min.) for adult females of P. persimilis to attack and kill N. californicus larva (U = 11.5; P < 0.001). The mean estimated attack time of A. swirskii and P. persimilis was 18.55±2.89 and 201.70±25.42 min., respectively. A. swirskii was more aggressive than P. persimilis against heterospecific larvae (U = 0.000; P < 0.001).

Table 1. Mean β-value for N. californicus adult female when offered con- and heterospecific larvae of P. persimilis simultaneously. N: N. californicus; P: P. Persimilis.

<table>
<thead>
<tr>
<th>Predator*</th>
<th>Prey**</th>
<th>( \beta ) mean±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. californicus</td>
<td>N</td>
<td>0.218±0.0745</td>
</tr>
<tr>
<td>N. californicus</td>
<td>P</td>
<td>0.782±0.0745</td>
</tr>
<tr>
<td>P. persimilis</td>
<td>N</td>
<td>0.523±0.0618</td>
</tr>
<tr>
<td>P. persimilis</td>
<td>P</td>
<td>0.477±0.0618</td>
</tr>
</tbody>
</table>

*Predator stage female
**Prey stage larvae

The mean predation index (β) for N. californicus on heterospecific larvae was higher than conspecific larvae in absence of T. urticae (U = 21.5, P < 0.001) and P. persimilis on heterospecific larvae was very close to
conspecific larvae in absence of *T. urticae* (*t* = -0.534, *df* = 30, *P* = 0.598) (Table 1). *N. californicus* adult female preferred heterospecific larvae significantly and *P. persimilis* did not show any preference in both larvae and chose both of them similar.

The mean predation index (β) for *A. swirskii* on heterospecific larvae was higher than conspecific larvae in absence of *T. urticae* (*t* = 3.710, *df* = 6, *P* = 0.00997) and *P. persimilis* was slightly higher on heterospecific larvae than conspecific larvae in absence of *T. urticae* (*U* = 75, *P* = 0.046) (Table 2).

Table 2. Mean β-value for *A. swirskii* adult female when offered cons- and heterospecific larvae of *P. persimilis* simultaneously. *A. A. swirskii*; *P. P. persimilis*.

<table>
<thead>
<tr>
<th>Predator*</th>
<th>Prey**</th>
<th>β mean±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. swirskii</em></td>
<td><em>A</em></td>
<td>0.294±0.0784</td>
</tr>
<tr>
<td><em>A. swirskii</em></td>
<td><em>P</em></td>
<td>0.706±0.0784</td>
</tr>
<tr>
<td><em>P. persimilis</em></td>
<td><em>A</em></td>
<td>0.369±0.0854</td>
</tr>
<tr>
<td><em>P. persimilis</em></td>
<td><em>P</em></td>
<td>0.630±0.0854</td>
</tr>
</tbody>
</table>

*Predator stage female
**Prey stage larva

**Discussion**

*A. swirskii* and *N. californicus* adult females were considered as highly aggressive intraguild predators of *P. persimilis* larvae. The attack time of *A. swirskii* against *P. persimilis* was significantly (*U* = 106.5, *P* = 0.012) shorter than that of *N. californicus*. The specialist predator, *P. persimilis* showed a very low aggressive behavior both against *N. californicus* and *A. swirskii* which is in consistent with Schausberger & Croft (2000) who demonstrated that specialist predators showed slight aggressiveness against heterospecific larvae. They measured both the survival time and survival rate of *N. californicus*, *P. macropilis* (Banks) and *P. persimilis* larvae when caged singly with adult *Galendromus occidentalis* (Nesbitt) as a specialist predator and no significant level of pairwise significance, likewise for *P. macropilis* and *P. persimilis* larvae when caged singly with *N. longispinosus* (Evans) (specialist on spider mite). Abad-Moyano et al. (2010) showed in their study *Euseius stipulatus* (Athias-Henriot) females were highly aggressive IG predators of *N. californicus* and *P. persimilis* larvae, it is in contrast of our result generalist predators are more aggressive than specialist predators.

Schausberger & Croft (2000) discussed that the hunger level would also affect the intensity of the predator aggressiveness in the guild. They showed that the lower hunger level in *T. pyri* would lead to a more moderate level of cannibalism in comparison with other generalist predators. We kept the species starved for 24 hours but as female of different species would experience different hunger levels despite equal periods of starvation (Schausberger & Croft 2000). It would be worthy to estimate and equalize the species real hunger level and evaluate its effect of their attack rate.

Abad-Moyano et al. (2010) stated that when the heterospecific prey (larvae) belonged to a facultative or non-feeding type might have been easier to be caught in comparison with obligatory feeding ones. They showed that catching small slowly moving larvae *N. californicus* (as Facultatively Feeding Larvae) and *P. persimilis* (as Non-Feeding Larvae), may have been easier than large quickly moving larvae such as *E. stipulatus* (as Obligate Feeding Larvae). This is in line with our results: The times of first attack on behalf of *P. persimilis* (NFL) against *N. californicus* and *A. swirskii* were about 6 (227 min.) and 11 (201 min.) fold higher than that in reverse.

*A. swirskii* killed a high number of prey larvae within the first 5 minutes of attack (60%) while no *P. persimilis* larvae was killed by *N. californicus* in this time. The rate of successful attack increased to 100% for *A. swirskii* during the next 15 minutes, while this rate was estimated as 75% for *N. californicus* for the same period of time. Schausberger & Croft (2000) also reported that the generalist predators *N. cucumeris*, *N. californicus* and *N. fallacis* had killed 75% and 100% of its heterospecific larvae within 1 and 6 hours, respectively.

The specialist predator, *P. persimilis* was the least aggressive among all. When *P. persimilis* females were considered as heterospecific predators, no successful attack was recorded during the first 30 minutes of experiment. The first killed *N. californicus* and *A. swirskii* larva were recorded from the 45–60th minutes of experiment (1.66%). The rate of successful attack was increased to 16% in the 2nd hour of experiment. This
is in line with Schausberger & Croft (2000) who demonstrated that larvae caged with specialist predator, *P. persimilis* had a higher survival chance in comparison with those caged by generalists.

The aim of prey preference study was to determine the preference of generalist and specialist predators at constant densities of con- and heterospecific larvae in absence of *T. urticae*. In our experiments, adult females of generalist predators *A. swirskii* and *N. californicus* vividly discriminated between con- and heterospecific larvae in absence of *T. urticae* and actually prefer to choice heterospecific larvae instead of conspecific larvae. Phytoseiid predators select prey species according to its profitability. Discriminating between con- and heterospecific larvae and having a preference for each one could be related to predation types (generalist vs. specialist) (Schausberger 1999).

Our result confirm that adult females of generalist predators *A. swirskii* and *N. californicus* fed more on heterospecific larvae than *P. persimilis* as specialist predator. In this regard, the results of (Monetti & Croft 1997; Palevsky 1997; Croft et al. 1998) showed that generalist predator *N. californicus* preferred to feed on heterospecific larvae when con- and heterospecific larvae were offered simultaneously. Other previous studies on generalist phytoseid species, including *Iphiseius degenerans* (Berlese), *N. fallacis*, *T. athiasae* Porath and Swirski, *T. pyri* and *Kammpodromus aberrans* (Oudemans) (Yao & Chant 1989; Monetti & Croft 1997; Palevsky 1997; Schausberger 1997, 1999a; Croft et al. 1998) showed that interspecific predation is higher than cannibalism. On the other hands, the specialist adult female of *P. persimilis* had more rates of cannibalism than interspecific predation. In our comparison we observed slight cannibalism in specialist predator compared with generalist predators. *P. persimilis* as a specialist predator was not able to discriminate between con- and heterospecific larvae and fed on both of them only occasionally. Momen & Abdel-Khalek (2009) in their study showed that *E. scutalis* and *T. swirskii* can discriminate heterospecific from conspecific prey and preferred to feed on hetero- than conspecific prey (Schausberger 2003). The results of MacRae & Croft (1997) showed that *T. pyri* as generalist predator preferred to feed on phytoseiid larvae when phytoseid larvae and *T. urticae* were offered simultaneously and in this situation *G. occidentalis* as specialist predator preferred *T. urticae* as prey. *P. persimilis* and *N. californicus* can feed on young stages of each other (Walzer and Schausberger 1999a; Akmak et al. 2006). *P. persimilis* suffered from intraguild predation less in comparison with *N. californicus* as long as the shared prey was present (Çakmak et al. 2006). Palevsky et al. (1999) showed that *T. athiasae*, had higher predation rate on heterospecific eggs than conspecific ones. Madadi et al. (2008) revealed that intraguild predation of *Orius albidipennis* (Reuter) on predatory mite eggs (*N. cucumeris*) only occurred in the absence of extraguild prey, whereas predatory mites were preyed on both in absence and presence of thrips as extraguild prey. Rasmey et al. (2004) showed that *A. swirskii* was able to fed and sustain oviposition when offered con- or heterospecific nymphs of phytoseiid mite *E. scutalis* and *Agistemus exertus* Gonzales as prey. They fed on conspecific protonymphs but the longevity, fecundity and the predation rates were shorter than that when the females fed on *T. urticae*.

The preference of predatory mites might depend on many factors such as plant architecture, prey stage preference and interaction between the pest and the predator (Pratt et al. 2002; Xu & Enkegard 2010). Long term studies on more realistic conditions are needed to clarify the preference of these phytoseiid species in suppressing prey in the presence of con- and heterospecific predators. Predator-predator interaction such as intraguild predation (IGP) and cannibalism are the most important factors that affect the development and coexistence of predator populations (Elgar 1990; Rosenheim et al. 1995; Sunderland et al. 1997; Schausberger & Walzer 2001), should be considered when multiple species were offered for persistence and disappear of one species in biological control.

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References


