

## *Tetranychus urticae* changes its oviposition pattern in the presence of the predatory mites, *Phytoseiulus persimilis* and *Typhlodromus bagdasarjani*

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**Abstract** Oviposition behaviors in herbivorous mites are affected by several factors *i.e.* food availability for juveniles and reduced predation risks. We used the twospotted spider mite, *Tetranychus urticae* Koch (Tetranychidae) to find out whether the previous presence of specialist/ generalist phytoseiid predator individuals, *Phytoseiulus persimilis* Athias-Henriot/ *Typhlodromus bagdasarjani* Wainstein & Arutunjan (here, direct effect) or their previous odour perception by prey (here, indirect effect) would affect *T. urticae* oviposition strategies. *Tetranychus urticae* female individuals were placed on a leaf disc in a plastic container with predators either on the same disc (direct presence of predator) or on the second disc (receiving odours related to a predator) in the same container. Getting experienced, the prey individuals transferred to the oviposition container to their oviposition pattern parameters get recorded. The ovipositing *T. urticae* were monitored in two experimental situations: 1. Receiving odours related to the predator- prey interaction from the second leaf disc in the same oviposition container during their oviposition period, and 2. Receiving no odour. Our results showed that when *T. urticae* females perceived the predator presence in their first container (with either predator species, both direct and indirect effect), they reduced their total egg distances, oviposition rates and oviposition periods significantly regardless of receiving odours related to prey-predator interactions during experiment. Receiving odours during oviposition, *T. urticae* females decreased their pairwise egg distances in at least 4 and at most 6 pairs of eggs, while when odours were absent during oviposition, the distances decreased in at least 2 and at most 3 pairs of eggs. The direct presence of *P. persimilis* reduced the prey oviposition period significantly more than that when *T. bagdasarjani* was present. The spider mites oviposition rate reduction was obviously more than that in the presence of *T. bagdasarjani*. The different effects of predator species on *T. urticae* egg distances were discussed.

## Zmiana wzoru składania jaj przez *Tetranychus urticae* w obecności drapieżnych roztoczy, *Phytoseiulus persimilis* i *Typhlodromus bagdasarjani*

Słowa kluczowe składanie jaj, przędziorki, drapieżnictwo, opieka rodzicielska, Phytoseiidae

**Streszczenie** Na zachowania związane ze składaniem jaj roztoczy roślinożernych wpływa kilka czynników między innymi dostępność pokarmu dla młodych osobników i zmniejszone ryzyko drapieżnictwa. Użyliśmy przędziorka *Tetranychus urticae* Koch (Tetranychidae), aby dowiedzieć się, czy obecność drapieżnika określonego typu (wyspecjalizowany w drapieżnictwie na *Tetranychus urticae* przedstawiciel drapieżnych dobroczynkowatych, *Phytoseiulus persimilis* Athias-Henriot i niewyspecjalizowany *Typhlodromus bagdasarjani* Wainstein & Arutunjan) wpływają na strategię składania jaj *T. urticae*. Następnie powtórzyliśmy eksperyment używając zapachu poprzednich ofiar tych drapieżników. Samice *Tetranychus urticae* umieszczono na krążku z liści w plastikowym pojemniku z drapieżnikami na tym samym krążku (bezpośrednia obecność drapieżnika) lub na drugim krążku (odbierającym zapachy związane z drapieżnikiem) w tym samym pojemniku. Po doświadczeniu, ofiary przenoszono do pojemnika, w którym samice składały jaja. Parametry związane ze składaniem jaj *T. urticae* monitorowano w dwóch grupach doświadczalnych: grupa eksperymentalna otrzymywała zapach związany z interakcją drapieżnik-ofiara, natomiast grupa kontrolna nie otrzymywała zapachu. Nasze wyniki wykazały, że gdy samice *T. urticae* dostrzegły obecność drapieżnika lub jego zapach (w przypadku obu gatunków drapieżników), znacznie zmniejszyły liczbę składanych jaj i odległości między składanymi jajami, a ponadto skracaly okres składania jaj, niezależnie od aplikowania zapachów związanych z interakcją między drapieżnikiem i ofiarą. Jednak aplikacja zapachu podczas składania jaj powodowała zmniejszenie odległości między składanymi jajami w od 4 do 6 par kolejno składanych jaj. W grupie kontrolnej, odległości zmniejszyły się w od 2 lub 3 parach kolejno składanych jaj. Bezpośrednia obecność *P. persimilis* skróciła okres składania jaj przez ofiarę znacznie bardziej niż obecność *T. bagdasarjani*. Zmniejszenie szybkości składania jaj przez przędziorki było wyraźnie większe niż w obecności *T. bagdasarjani*.

## Introduction

Animals with a range of specialist and non-specialist predators are confronted with many time and energy costing risks during their foraging behavior. The behavioral decisions made under the risk of predation are more imperative than those made to detect food (Lima, Dill, 1990). Many organisms show defensive or evasive behaviors when they receive chemical information related to their predators (direct cues of predation risk) or from the conspecifics injured by those predators (indirect cues of predation risk). The prey different reactions in these situations depend on several factors i.e. how familiar the prey is with the alerting cues, the predator risk level and the prey strategies to avoid predator (Grostal, Dicke, 1999). These crucial traits that influence the prey behavior, distribution and whole fitness, could also lead to a range of new indirect interactions in the food web (Abrams, 1996).

Failing to detect a high-risk predator increases the encounter rate of prey with predator which might have important implications on its survival and reproductive success. Several studies have demonstrated that once a predator has been detected, prey changes its behavior so that decrease its vulnerability. The crayfish, *Paranephrops zealandicus* (Koura) reduced its stationary and walking behavior when it received chemicals related to eel (*Anguilla dieffenbachia*) (Shave, Townsend, Crowl, 1994). *Daphnia magna* Straus, respond to chemicals related to its injured conspecifics (crushed *Daphnia*) by formation of aggregation and vertical distribution towards the bottom (Pijanowska, 1997). The fruit flies (*Rhagoletis basiola* (Osten Sacken), Tephritidae) delayed their oviposition when received cues related to their egg parasitoid (Hoffmeister, Roitberg, 1997). Dias

et al. (2016) demonstrated that the response of prey to the cues related to dangerous and harmless predators could be different.

Several studies have demonstrated that when a predator and its con- or hetero-specific competitor are present together, the former should adopt strategies in order to decrease the risk of its offspring being preyed upon. Montserrat et al. (2007) showed that females of *Neoseiulus cucumeris* (Oudemans) reduced oviposition by retaining eggs inside their body when exposed to *Iphiseius degenerans* (Berlese). *Amblyseius swirskii* (Athias-Henriot) could anticipate the possible counterattacks on behalf of *Frankliniella occidentalis* Pergande and avoided ovipositing near thrips (de Almedia, Janssen, 2013). *I. degenerans* oviposits away from their food source (pollen) when the predator of its eggs, *F. occidentalis* was present on the flower (Faraji, Janssen, van Rijn, Sabelis, 2000). Spider mites are known to show anti-predator responses through behaviors such as patch avoidance, induced diapause, reduction of oviposition, producing dense web and moving away from the patch which the predator is present in (Pallini, Janssen, Sabelis, 1999; Choh, Takabayashi, 2006; Kroon, Veenendaal, Bruin, Egas, Sabelis, 2008; Shimoda, Kishimoto, Takabayashi, Amano, Dicke, 2009; Lemos et al., 2010). Dittmann and Schausberger (2017) documented that the aggregated spider mites were less encountered by *Phytoseiulus persimilis* Athias-Henriot in comparison with the scattered ones. They suggested that more aggregation (inter-individual distance reduction) in *T. urticae* would lead to more efficacious anti-predator behaviours. Dias et al. (2016) reported that *Tetranychus evansi* Baker and Pritchard oviposited less and escaped more when their dangerous predator *Phytoseiulus longipes* Evans was present on the same patch. They concluded that spider mite antipredator behaviours varied with the level of the predator danger. Hackl and Schausberger (2014) were the first who demonstrated that experience and learning could modulate *T. urticae* anti-predator behaviours. They reported that previous predator experience would lead to a balanced response of *T. urticae* to *P. persimilis* cues in the shape of oviposition delay and activity reduction, but not reducing the oviposition rate. They also did not discuss whether the predator perception by *T. urticae* would lead to the prey oviposition pattern.

*Typhlodromus bagdasarjani* Wainstein & Arutunjan is a generalist indigenous phytoseiid mite (Type III) with a wide distribution in the Middle East, especially in the orchards of Iran and reported from plants infested by tetranychids and eriophyids as well as insect pests such as thrips and whiteflies. Various plant exudates, as well as honeydew, may serve as supplements which could increase its reproduction potential in food scarcity. *T. bagdasarjani* could be well adapted to warm climates (Farazmand, Fathipour, Kamali, 2013; Moghadasi, Saboori, Allahyari, Zahedi Golpayegani, 2013; McMurtry, De Moraes, Sourassou, 2013). *Phytoseiulus persimilis* Athias-Henriot is a specialist (Type I) commercialized predatory mite that is commonly used in ornamental greenhouses to control spider mites. This predatory mite has a short generation time with high fecundity and its post-larval stages are able to attack all stages of *T. urticae* (Moghadasi et al., 2013; Landeros, Guevara, Badii, Flores, Pamanes, 2004; Pizzol, Poncet, Hector, Ziegler, 2006).

Here, we have investigated the direct and indirect effects of the predatory mites, *P. persimilis* and *T. bagdasarjani* on the oviposition rate, distances between eggs and oviposition period of *T. urticae*. Recording the direct effects, we put the predator female individuals (each species separately) on the same leaf disc which *T. urticae* was present. For indirect effects, no predator was introduced to the spider mite leaf disc, but the ovipositing spider mites received the odours related to interacting prey- predator from the nearby leaf disc in the same container. We tested whether continuing to receive odours during oviposition could also affect *T. urticae* oviposition behavior. We expected that spider mites should reduce the distances between eggs and increase

their oviposition period when perceived the predator effects. The effect of predator species on the prey strategies is discussed.

## Materials and Methods

### Plants and mites

Rose plants (*Rosa hybrida* cv. 'blarodje' (Rosaceae)) used in this study were grown in beds under commercial conditions (Cocopeat: Perlite; 60: 40%) in the greenhouse. Plants were pruned and planted in large plastic pots (25 cm top diameter, 40 cm depth and 20 cm bottom diameter) at  $25 \pm 2^\circ\text{C}$ ,  $65 \pm 10\%$  RH and 16L: 8D hour photoperiod. Spider mites, *T. urticae*, were originally collected from infested lima bean cultures in the acarology laboratory at the Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran. Spider mites were transferred onto detached rose leaves placed upside down on water-saturated cotton wool in transparent plastic containers ( $20 \times 10 \times 4$  cm). The rearing containers were maintained in controlled conditions at  $24 \pm 2^\circ\text{C}$ ,  $60 \pm 5\%$  RH, and 16L: 8D hour photoperiod, since three months prior to experiments.

The predatory mites, *T. bagdasarjani* were collected from black mulberry trees at the campus of Tarbiat Modares University, Tehran, Iran. *Phytoseiulus persimilis* culture was initially obtained from laboratory stock culture reared at the Acarology laboratory at the Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran. The predatory mites were kept on masses of detached rose leaves deposited upside down on a plastic sheet placed on a water saturated sponge. The plastic sheet was surrounded by napkin tapes which were put into the water from another side so that the predatory mites could drink water. The rearing units were kept at controlled conditions ( $25 \pm 1^\circ\text{C}$ ,  $75 \pm 5\%$  RH and 16L: 8D hour photoperiod) in a growth chamber. All experiments were carried out at  $25\text{--}26^\circ\text{C}$ ,  $75\text{--}80\%$  RH, and 16L: 8D hour photoperiod in growth chamber.

### General experimental conditions

The experimental units consisted of fresh detached rose leaf discs ( $2 \times 2$  cm<sup>2</sup>) placed upside down on semi-divided water-saturated sponges in a porous (8 pore) transparent plastic container (Figure 1). Each pair of cubic sponges was adjusted in a way that the cubes were spaced 15 mm

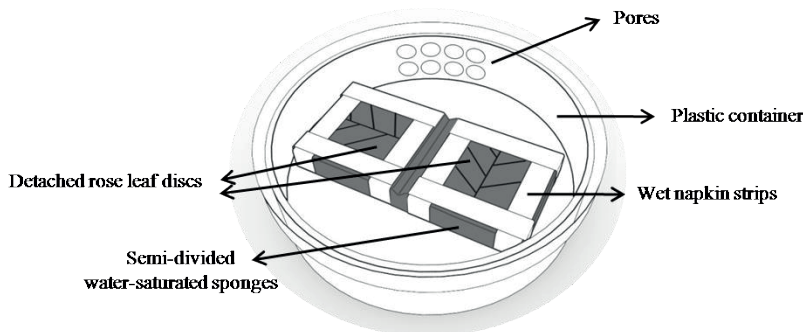


Figure 1. The experimental unit

from each other. Wet napkin strips were placed around the leaf margins in order to prevent the mites from escaping. Here, the preconditioning plastic container and the oviposition container were considered as the places for the spider mites to get experienced with odors and to check their oviposition behaviors respectively. Depending on the experiments, one of or both of the leaf discs in each container were used.

## Experiments

The oviposition pattern of *T. urticae* when experienced the predator presence (Direct effect)

Quiescent *T. urticae* female deutonymphs were selected from the main culture and put on separate leaf discs. After 24 hours, adult same-aged males were introduced to the females for mating. Newly mated *T. urticae* females were selected randomly (Choh, Uefune, Takabayashi, 2010). Two same-aged predator females (4 days old, predation rate at pick, unpublished data) and 10 same-aged *T. urticae* mated females were introduced to a plastic container (one of the pairwise leaf discs) mentioned above. 24 hours after the predator-prey interactions, one alive *T. urticae* female was selected randomly and transferred to a new leaf disc singly in a separate container (namely oviposition container) as treatment. *Tetranychus urticae* mated females (same-aged with those in treatment) which had not experienced the predator presence (in their preconditioning container) were transferred to a new leaf disc (namely oviposition container) singly and considered as control. This experiment was conducted in two situations: 1) When *T. urticae* females did not receive the odours related to predator-prey interactions in their oviposition container (Figure 2), and 2) when *T. urticae* females received odours related to predators and prey interactions from the second leaf disc in the same (oviposition) container (Figure 3). The second leaf discs both in the preconditioning (experiencing) and the oviposition container was prepared by introducing three same-aged female predators along with 10 ovipositing *T. urticae* 24 hours prior to monitoring got started, so that the prey and predators had sufficient time to interact. We kept recording data until

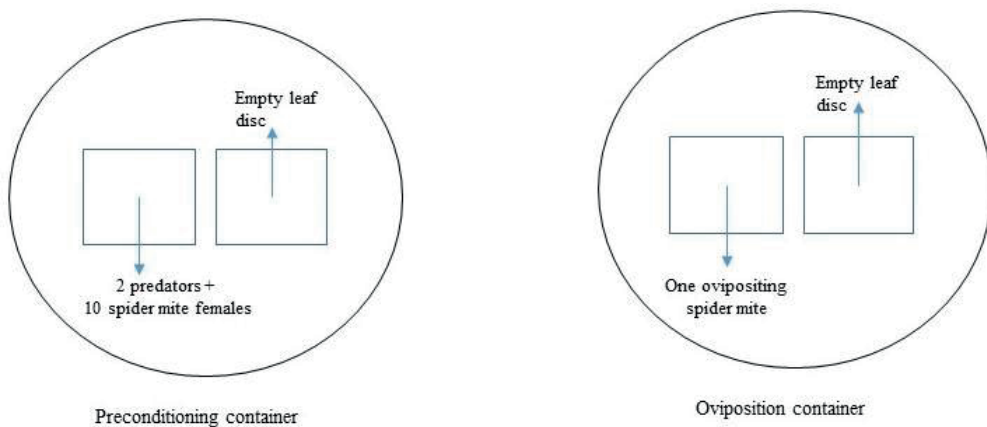


Figure 2. The experimental unit for recording the oviposition behavior of *T. urticae* females when received no odours related to interacting prey and predators (Direct effect)

the female spider mites died. Data were recorded for *T. urticae* as follows: a) Total number of eggs each female oviposited till its death, b) Pairwise and total egg distances by regular monitoring, c) The oviposition period of spider mite females. The oviposition priority of eggs was shown by different watercolor spots put beside them. Distances were measured by ruler under binocular microscope (Schausberger, 2005). Each experiment was replicated 20 times.

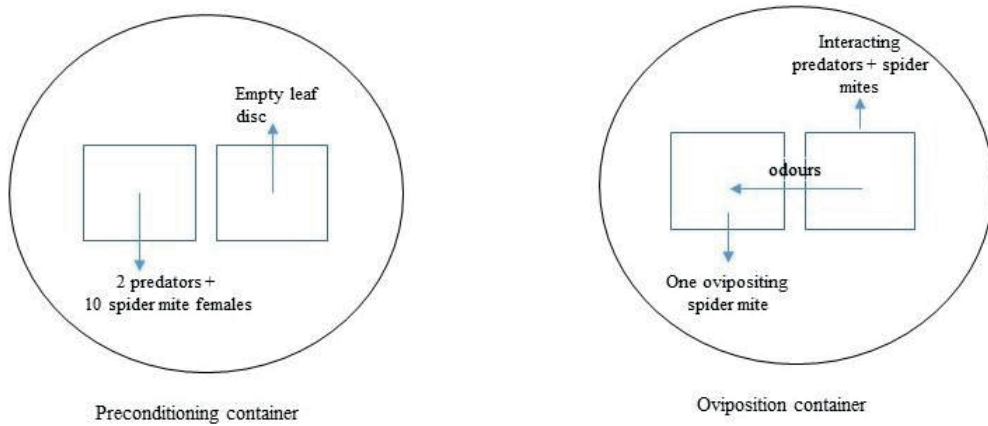


Figure 3. The experimental unit for recording the oviposition behavior of *T. urticae* females when received odours related to interacting prey and predators from the second leaf disc (Direct effect)

### The oviposition pattern of *T. urticae* when experienced volatiles related to the predator (Indirect effect)

Two same-aged predator females (4 days old, predation rate at the pick, unpublished data) and 10 same-aged *T. urticae* mated females were introduced into a plastic container (one of the pairwise leaf discs). The second leaf disc of the container was infested by 10 *T. urticae* mated females (without predators). As both discs were kept in the same container (mentioned above), the spider mite females of the second leaf disc received the odours related to the interactions among their conspecifics with the predators in the first leaf disc. After 24 hours, one *T. urticae* was selected from the second leaf disc randomly and transferred to a new leaf disc in a new (oviposition) container (treatment). *Tetranychus urticae* mated females (same-aged with those in treatment) which had just experienced the odours related to conspecifics interactions, were transferred to their oviposition container singly and considered as control. This experiment was conducted in two situations: 1) When *T. urticae* females did not receive the odours related to predator-prey interactions in their second (oviposition) container, and 2) when *T. urticae* female in the oviposition container (during oviposition) received odours related to predator-prey interactions from the second leaf disc of the same container. We kept recording data until the female spider mites died. Data were recorded for *T. urticae* as follows: a) The total number of eggs each female oviposited till its death, b) pairwise and total egg distances by regular monitoring (just for the first seven oviposited eggs as recording such data for the whole (30–40) eggs would be time-consuming), c) The oviposition period of spider mite females. The oviposition priority of eggs

was shown by different watercolor spots put beside them. Distances were measured by ruler under binocular. Each experiment was replicated 20 times.

## Data analysis

The oviposition parameters of *T. urticae* in the presence of *P. persimilis* were recorded simultaneously with those in the presence of *T. bagdasarjani*. Independent sample-test was performed to compare the total number of eggs, oviposition period and pairwise and total egg distance between treatments as well as between each treatment and control using SPSS 16.

## Results

### The oviposition pattern of *T. urticae* when experienced the predator presence (Direct effect)

#### Receiving no odours in the oviposition container during oviposition

When *T. urticae* females experienced the predator (either *P. persimilis* or *T. bagdasarjani*) presence in their preconditioning container, they reduced pairwise distances between their first three eggs significantly (Tables 1 and 2,  $P < 0.01$ ). The pairwise distances between their 4<sup>th</sup> to 7<sup>th</sup> eggs did not show any significant difference ( $P > 0.05$ ). *Tetranychus urticae* total egg distances were significantly shorter when the females experienced the predator presence before starting oviposition (Table 1,  $P < 0.05$ ) (Table 2,  $P < 0.01$ ). Also, *T. urticae* females laid significant fewer eggs when they previously had perceived the predator presence (Tables 1 and 2,  $P < 0.01$ ). The oviposition periods also decreased when the females experienced the predator presence prior to oviposition (Tables 1 and 2,  $P < 0.01$ ).

Table 1. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced *P. persimilis* presence in their preconditioning container

Source of variation	Predator presence (Mean ± SE)	Control (Mean ± SE)	<i>P</i>
Pairwise egg distances	1–2	7.7 ±0.73	0.005**
	2–3	7.45 ±0.71	0.022**
	3–4	6.57 ±0.74	0.000**
	4–5	7.72 ±0.75	0.816
	5–6	8.4 ±0.42	0.641
	6–7	8.27 ±0.42	0.898
Total egg distance (1–7)	46.12 ±2.65	57.58 ±3.31	0.010*
Mean of egg distances	7.67 ±0.44	9.59 ±0.55	0.010*
Total number of eggs	24.15 ±1.02	34.7 ±1.69	0.000**
Oviposition period	10.45 ±0.11	11.65 ±0.13	0.000**



Table 2. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced *T. bagdasarjani* presence in their preconditioning container

Source of variation	Predator presence (Mean ± SE)	Control (Mean ± SE)	<i>P</i>	
Pairwise egg distances	1–2	7.22 ±0.69	11.8 ±1.18	0.002**
	2–3	6.82 ±0.82	10.4 ±1.02	0.009**
	3–4	7.45 ±0.69	11.22 ±0.88	0.002**
	4–5	8.07 ±0.62	8.02 ±1.04	0.967
	5–6	8.4 ±0.75	7.95 ±0.84	0.697
	6–7	7 ±0.66	8.17 ±0.65	0.213
Total egg distance (1–7)	44.97 ±2.99	57.58 ±3.31	0.010*	
Mean of egg distances	7.49 ±0.49	9.59 ±0.55	0.008*	
Total number of eggs	25.55 ±1.38	34.7 ±1.69	0.000**	
Oviposition period	10.75 ±0.09	11.65 ±0.13	0.000**	

The pairwise estimated distances from the 1<sup>st</sup> to the 7<sup>th</sup> *T. urticae* eggs did not differ significantly when they experienced either *P. persimilis* or *T. bagdasarjani*. This was also true for their total egg distances (Table 3,  $P < 0.05$ ). Although the total number of *T. urticae* eggs was lower in the presence of *P. persimilis* in comparison with in the presence of *T. bagdasarjani*, no significant difference was observed between them ( $P < 0.05$ ). The oviposition period of females also did not show any significant difference in the presence of each of the predators (Table 3,  $P > 0.05$ ).

Table 3. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced either *P. persimilis* or *T. bagdasarjani* presence in their preconditioning container

Source of variation	<i>P. persimilis</i> presence (Mean ± SE)	<i>T. bagdasarjani</i> presence (Mean ± SE)	<i>P</i>	
Pairwise egg distances	1–2	7.7 ±0.73	7.22 ±0.69	0.637
	2–3	7.45 ±0.71	6.82 ±0.82	0.569
	3–4	6.57 ±0.74	7.45 ±0.69	0.395
	4–5	7.72 ±0.75	8.07 ±0.62	0.721
	5–6	8.4 ±0.42	8.4 ±0.75	1.000
	6–7	8.27 ±0.42	7 ±0.66	0.113
Total egg distance (1–7)	46.12 ±2.65	44.97 ±2.99	0.775	
Mean of egg distances	7.69 ±0.44	7.49 ±0.49	0.778	
Total number of eggs	24.15 ±1.02	25.55 ±1.38	0.422	
Oviposition period	10.45 ±0.11	10.75 ±0.09	0.055	

### Receiving predator-prey odours during oviposition

In the treatments which *T. urticae* females not only had experienced the predator (*P. persimilis*) presence in their preconditioning container, but also received odours related to predator-prey interactions from the second leaf disc of the oviposition container (during oviposition), the pairwise distances between the 1<sup>st</sup> to the 7<sup>th</sup> eggs were decreased whereas the distance reduction between the 4<sup>th</sup> and 5<sup>th</sup> eggs was not significant (Table 4). *Tetranychus urticae* total egg distance,



the total number of eggs and oviposition period were significantly reduced by receiving predator-prey odours during oviposition (Table 4,  $P < 0.01$ ).

Table 4. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced *P. persimilis* in their preconditioning container and received predator-prey odours during oviposition

Source of variation	Predator presence (Mean ± SE)	Control (Mean ± SE)	<i>P</i>	
Pairwise egg distances	1–2	5 ± 0.69	10.7 ± 1.14	0.000**
	2–3	6.4 ± 0.66	10.27 ± 0.91	0.001**
	3–4	5.5 ± 0.93	10.97 ± 0.93	0.000**
	4–5	5.9 ± 0.99	8.6 ± 0.93	0.054
	5–6	5.3 ± 0.53	8.7 ± 0.67	0.000**
	6–7	6.8 ± 0.58	8.45 ± 0.52	0.041*
Total egg distance (1–7)	34.9 ± 3.43	57.7 ± 3.45	0.000**	
Mean of egg distances	5.82 ± 0.57	9.62 ± 0.57	0.000**	
Total number of eggs	19.4 ± 0.59	34.45 ± 1.7	0.000**	
Oviposition period	10.6 ± 0.15	11.7 ± 0.10	0.000**	

Receiving odours related to *T. bagdasarjani*-*T. urticae* interactions from the second leaf disc of the oviposition container (during oviposition), *T. urticae* females reduced the pairwise distances between their 1<sup>st</sup> to 4<sup>th</sup> and 6<sup>th</sup> to 7<sup>th</sup> eggs significantly when they experienced *T. bagdasarjani* in their preconditioning container (Table 5). Although the distances between the eggs 4<sup>th</sup> to 5<sup>th</sup> and 5<sup>th</sup> to 6<sup>th</sup> were reduced in comparison with control, the differences were not significant. *Tetranychus urticae* total egg distance, the total number of eggs and oviposition period were significantly reduced by receiving predator-prey odours during oviposition (Table 5,  $P < 0.01$ ).

Table 5. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced *T. bagdasarjani* in their preconditioning container and received predator-prey odours during oviposition

Source of variation	Predator presence (Mean ± SE)	Control (Mean ± SE)	<i>P</i>	
Pairwise egg distances	1–2	5.95 ± 1.04	10.7 ± 1.14	0.004**
	2–3	6.55 ± 1.04	10.27 ± 0.91	0.011*
	3–4	7.12 ± 0.96	10.97 ± 0.93	0.006**
	4–5	6.72 ± 0.87	8.6 ± 0.93	0.148
	5–6	7.95 ± 0.92	8.7 ± 0.67	0.514
	6–7	6.07 ± 0.70	8.45 ± 0.52	0.010*
Total egg distance (1–7)	40.37 ± 3.55	57.7 ± 3.45	0.001**	
Mean of egg distances	6.73 ± 0.59	9.62 ± 0.57	0.001**	
Total number of eggs	24.55 ± 1.7	34.45 ± 1.7	0.000**	
Oviposition period	10.75 ± 0.12	11.7 ± 0.10	0.000**	

The pairwise estimated distances from the 1<sup>st</sup> to the 7<sup>th</sup> *T. urticae* eggs did not differ significantly when they experienced either *P. persimilis* or *T. bagdasarjani*. This was also true for

their total egg distances (Table 6,  $P < 0.05$ ). The total number of *T. urticae* eggs was lower in the presence of *P. persimilis* ( $P < 0.05$ ). The oviposition period of females also did not show any significant difference in the presence of each of the predators (Table 6,  $P > 0.05$ ).

Table 6. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced either *P. persimilis* or *T. bagdasarjani* presence in their preconditioning container and received the same predator-prey odours during oviposition

Source of variation	<i>P. persimilis</i> presence (Mean $\pm$ SE)	<i>T. bagdasarjani</i> presence (Mean $\pm$ SE)	<i>P</i>
Pairwise egg distances	1–2	5 $\pm$ 0.69	0.454
	2–3	6.4 $\pm$ 0.66	0.904
	3–4	5.5 $\pm$ 0.93	0.232
	4–5	5.9 $\pm$ 0.99	0.535
	5–6	5.3 $\pm$ 0.53	0.017*
	6–7	6.8 $\pm$ 0.58	0.430
Total egg distance (1–7)	34.9 $\pm$ 3.43	40.37 $\pm$ 3.55	0.274
Mean of egg distances	5.82 $\pm$ 0.57	6.73 $\pm$ 0.59	0.274
Total number of eggs	19.4 $\pm$ 0.59	24.55 $\pm$ 1.7	0.007*
Oviposition period	10.6 $\pm$ 0.15	10.75 $\pm$ 0.12	0.448

### The oviposition pattern of *T. urticae* when received odours related to the predator-prey interactions in their preconditioning container (Indirect effect)

#### Receiving no odours in the oviposition container during oviposition

When *T. urticae* females experienced the presence of *P. persimilis* in their preconditioning container, they reduced their pairwise distances between their 1<sup>st</sup> and 2<sup>nd</sup> ( $P < 0.05$ ) and 3<sup>rd</sup> and 4<sup>th</sup> ( $P < 0.01$ ) eggs significantly (Table 7). The pairwise distances between their 4<sup>th</sup> to 7<sup>th</sup> eggs did not show any significant difference ( $P > 0.05$ ) and the distances between 2<sup>nd</sup> and 3<sup>rd</sup> eggs did likewise. *Tetranychus urticae* total egg distance was significantly shorter when the females had experienced *P. persimilis* presence prior to oviposition (Table 7,  $P < 0.05$ ), also *T. urticae* females preferred to lay significant fewer eggs when they previously had perceived the predator presence (Table 7,  $P < 0.01$ ). The oviposition period also decreased when the female spider mites had experienced *P. persimilis* prior to oviposition (Table 7,  $P < 0.01$ ).

When *T. urticae* females experienced the presence of *T. bagdasarjani* in their preconditioning container, they reduced their pairwise distances between their 1<sup>st</sup> to 3<sup>rd</sup> eggs significantly (Table 8,  $P < 0.05$ ). The pairwise distances between their 4<sup>th</sup> to 7<sup>th</sup> eggs did not show any significant difference ( $P > 0.05$ ). *Tetranychus urticae* total egg distance was significantly shorter when the females had experienced *T. bagdasarjani* presence prior to oviposition (Table 8,  $P < 0.05$ ), also *T. urticae* females preferred to lay significant fewer eggs when they previously had perceived the predator presence (Table 8,  $P < 0.01$ ). The oviposition period also decreased when the female spider mites had experienced *T. bagdasarjani* prior to oviposition (Table 8,  $P < 0.01$ ).

Table 7. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when received odours related to predator (*P. persimilis*)-prey interactions in their preconditioning container

Source of variation	Predator presence (Mean ± SE)	Control (Mean ± SE)	<i>P</i>
Pairwise egg distances	1–2	8.2 ±0.82	0.028*
	2–3	7.82 ±0.79	0.066
	3–4	6.9 ±0.88	0.001*
	4–5	8.15 ±0.79	0.311
	5–6	9.07 ±0.51	0.102
	6–7	8.42 ±0.59	0.583
Total egg distance (1–7)	48.57 ±2.68	58.87 ±3.41	0.023*
Mean of egg distances	8.09 ±0.45	9.81 ±0.57	0.023*
Total number of eggs	22.7 ±0.75	35.35 ±1.68	0.000**
Oviposition period	10.45 ±0.15	12.2 ±0.18	0.000**

Table 8. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when received odours related to predator (*T. bagdasarjani*)-prey interactions in their preconditioning container

Source of variation	Predator presence (Mean ± SE)	Control (Mean ± SE)	<i>P</i>
Pairwise egg distances	1–2	8.1 ±0.71	0.017*
	2–3	7 ±0.77	0.015*
	3–4	8.27 ±0.87	0.021*
	4–5	9.12 ±0.79	0.788
	5–6	9.07 ±0.84	0.178
	6–7	7.35 ±0.79	0.159
Total egg distance (1–7)	48.92 ±2.69	58.87 ±3.41	0.028*
Mean of egg distances	8.15 ±0.45	9.81 ±0.57	0.028*
Total number of eggs	26.5 ±1.43	35.35 ±1.68	0.000**
Oviposition period	10.6 ±0.13	12.2 ±0.18	0.000**

Table 9. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when experienced odours related to predator (*P. persimilis* /*T. bagdasarjani*)-prey interactions in their preconditioning container

Source of variation	<i>P. persimilis</i> presence (Mean ± SE)	<i>T. bagdasarjani</i> presence (Mean ± SE)	<i>P</i>
Pairwise egg distances	1–2	8.2 ±0.82	0.927
	2–3	7.82 ±0.79	0.461
	3–4	6.9 ±0.88	0.273
	4–5	8.15 ±0.79	0.392
	5–6	9.07 ±0.51	1.000
	6–7	8.42 ±0.59	0.284
Total egg distance (1–7)	48.57 ±2.68	48.92 ±2.69	0.927
Mean of egg distances	8.09 ±0.45	8.15 ±0.45	0.926
Total number of eggs	22.7 ±0.75	26.5 ±1.43	0.024*
Oviposition period	10.45 ±0.15	10.6 ±0.13	0.466

The pairwise estimated distances from the 1<sup>st</sup> to the 7<sup>th</sup> *T. urticae* eggs did not differ significantly between the treatments which received odours related to *P. persimilis* or *T. bagdasarjani*. It was also happened for their total egg distances (Table 9,  $P < 0.05$ ). The total number of *T. urticae* eggs was lower in the presence of *P. persimilis* ( $P < 0.05$ ). The oviposition period of females also did not show any significant difference in the presence of each of the predators (Table 9,  $P > 0.05$ ).

### Receiving predator-prey odours during oviposition

In the treatments which *T. urticae* females not only had experienced the predator (*P. persimilis*) presence in their preconditioning container but also received odours related to predator-prey interactions from the second leaf disc of the oviposition container (during oviposition), the pairwise distances between the 1<sup>st</sup> to the 7<sup>th</sup> eggs were decreased significantly (Table 10). *Tetranychus urticae* total egg distance, the total number of eggs and oviposition period were significantly reduced by receiving predator-prey odours during oviposition (Table 10,  $P < 0.01$ ).

Table 10. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when received odours related to predator (*P. persimilis*)-prey interactions in their preconditioning and oviposition containers

Source of variation	Predator presence (Mean $\pm$ SE)	Control (Mean $\pm$ SE)	<i>P</i>	
Pairwise egg distances	1–2	5.17 $\pm$ 0.71	10.15 $\pm$ 1.34	0.002**
	2–3	6.05 $\pm$ 0.61	10.32 $\pm$ 0.93	0.000**
	3–4	4.85 $\pm$ 0.83	10.7 $\pm$ 1.11	0.000**
	4–5	5.87 $\pm$ 0.80	8.46 $\pm$ 0.78	0.026*
	5–6	4.72 $\pm$ 0.57	8.22 $\pm$ 0.69	0.000**
	6–7	6.95 $\pm$ 0.57	8.57 $\pm$ 0.55	0.049*
Total egg distance (1–7)	33.62 $\pm$ 2.73	56.44 $\pm$ 3.16	0.000**	
Mean of egg distances	5.6 $\pm$ 0.45	9.41 $\pm$ 0.53	0.000**	
Total number of eggs	19.2 $\pm$ 0.71	33.55 $\pm$ 1.77	0.000**	
Oviposition period	10.15 $\pm$ 0.21	11.4 $\pm$ 0.15	0.000**	

Receiving odours related to *T. bagdasarjani*-*T. urticae* interactions during oviposition, *T. urticae* females reduced the pairwise distances between their 1<sup>st</sup> to 4<sup>th</sup> and 6<sup>th</sup> to 7<sup>th</sup> eggs significantly when they experienced *T. bagdasarjani* in their preconditioning container (Table 11). Although the distances between the eggs 4<sup>th</sup> to 5<sup>th</sup> and 5<sup>th</sup> to 6<sup>th</sup> were reduced in comparison with control, the differences were not significant. *Tetranychus urticae* total egg distance, the total number of eggs and oviposition period were significantly reduced by receiving predator-prey odours during oviposition (Table 11,  $P < 0.01$ ).

The pairwise estimated distances from the 1<sup>st</sup> to the 7<sup>th</sup> *T. urticae* eggs did not differ significantly ( $P > 0.05$ ) except the distances between the 5<sup>th</sup> and 6<sup>th</sup> eggs ( $P < 0.01$ ) between the treatments which received odours related to *P. persimilis* and *T. bagdasarjani*. It was also happened for their total egg distances (Table 12,  $P > 0.05$ ). The total number of *T. urticae* eggs was lower in the presence of *P. persimilis* ( $P < 0.05$ ). The oviposition period of females also did not show any significant difference in the presence of each of the predators (Table 12,  $P > 0.05$ ).

Table 11. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when received odours related to predator (*T. bagdasarjani*)-prey interactions in their preconditioning and oviposition containers

Source of variation		Predator presence (Mean ± SE)	Control (Mean ± SE)	P
Pairwise egg distances	1–2	5.75 ±1.05	10.15 ±1.34	0.014*
	2–3	6.62 ±1.07	10.32 ±0.93	0.013*
	3–4	6.57 ±1.09	10.7 ±1.11	0.012*
	4–5	6.57 ±1.07	8.46 ±0.78	0.162
	5–6	7.67 ±0.89	8.22 ±0.69	0.629
	6–7	6.47 ±0.72	8.57 ±0.55	0.026*
Total egg distance (1–7)		39.67 ±3.57	56.44 ±3.16	0.001**
Mean of egg distances		6.61 ±0.59	9.41 ±0.53	0.001**
Total number of eggs		23.75 ±1.66	33.55 ±1.77	0.000**
Oviposition period		10.15 ±0.18	11.4 ±0.15	0.000**

Table 12. The total number of eggs, egg distances (mm) and oviposition period (day) of *T. urticae* females when received odours related to predator (*P. persimilis* /*T. bagdasarjani*)-prey interactions in their preconditioning and oviposition containers

Source of variation		<i>P. persimilis</i> presence (Mean ± SE)	<i>T. bagdasarjani</i> presence (Mean ± SE)	P
Pairwise egg distances	1–2	5.17 ±0.71	5.75 ±1.05	0.652
	2–3	6.05 ±0.61	6.62 ±1.07	0.643
	3–4	4.85 ±0.83	6.57 ±1.09	0.217
	4–5	5.87 ±0.80	6.57 ±1.07	0.604
	5–6	4.72 ±0.57	7.67 ±0.89	0.008*
	6–7	6.95 ±0.57	6.47 ±0.72	0.608
Total egg distance (1–7)		33.62 ±2.73	39.67 ±3.57	0.187
Mean of egg distances		5.6 ±0.45	6.61 ±0.59	0.187
Total number of eggs		19.2 ±0.71	23.75 ±1.66	0.016
Oviposition period		10.15 ±0.21	10.15 ±0.18	1.000

## Discussion

Our experiments showed that when *T. urticae* females perceived the presence of a predator (either *P. persimilis* or *T. bagdasarjani*) directly in their predonditioning container, they reduced their oviposition rate, either when they received the odours related to predator during oviposition or even when no signal related to predator was present in their oviposition container. Our suggestion is that the spider mites here have had direct (predator cues) and indirect (dead conspecifics) means of predation risk recognition. This is in consistent with Grostal and Dicke (1999) who demonstrated that fewer spider mites foraged and laid eggs on predator exposed discs in comparison with the discs with intact conspecifics. Lemos et al. (2010) also demonstrated that although *Tetranychus evansi* Baker & Pritchard web mediated anti-predator behavior, the prey

did not produce denser webs when received cues related to their predator, *Phytoseiulus longipes* Evans, but laid more eggs in the web far from the predator foraging area.

According to our observations, *T. urticae* females put significantly fewer eggs when perceived the presence of *P. persimilis* (in their preconditioning container) in comparison with when *T. bagdasarjani* (an indigenous species) was present. Our interpretation is that *T. urticae* females interacted with each of the predator species for 24 hours before their oviposition pattern started to be recorded. During this period, *T. bagdasarjani* might have been recognized as a less harmful predator or a predator that could not deal with the prey web structure as well as *P. persimilis*. This probable short time experience (Hackl, Schuasberger, 2014) could lead to a higher oviposition rate of *T. urticae* in the oviposition container especially when no predator (*T. bagdasarjani*) or no cues related to predator was present in. This is similar to Lemos et al. (2010) who demonstrated that some predators (namely *P. persimilis*) could cope with the silken web produced by their prey. As far as we know, no published data is present about the reaction of *T. bagdasarjani* to *T. urticae* web structure.

In the treatments which *T. urticae* females not only had experienced the predator (*P. persimilis*/ *T. bagdasarjani*) presence in their preconditioning container but received odours related to predator-prey interactions in their oviposition container, they reduced their oviposition rate remarkably. This reduction was more perceptible when *P. persimilis* was chosen as predator species (approx. 44% in comparison with control). Although again the significant reduction of *T. urticae* oviposition rate was clear in the presence of *T. bagdasarjani* (25.55 ±6.2) receiving odours during oviposition did not affect the reduction of oviposition rate (24.55 ±7.6) significantly ( $t = 0.455$ ,  $df = 38$ ,  $P = 0.652$ ).

Receiving odours related to predator-prey interactions in the preconditioning container (instead of predator direct presence) led to a significant reduction in *T. urticae* oviposition rates both when the ovipositing females did not receive any odour in their oviposition container and when they still perceived cues related to predator-prey interactions during oviposition. This is similar to Skaloudova, Zemek and Krivan (2007) who demonstrated that prey reduced its activities (i.e. searching for food) when received the cues related to its predator, so that the physiological changes, happened due to food shortage, reduced its oviposition rate. They also exposed *T. urticae* to various cues of predator and observed that as much as the risk would increase the oviposition rate would decrease. Choh et al. (2010) also confirmed that spider mites laid less egg in the presence of predators, although the predator cues alone (without the prey presence) could not elicit such a response in spider mites.

In our experiments, the significant gap between the oviposition rates in the presence of odours related to *P. persimilis*-*T. urticae* interactions and in the presence of odours related to *T. bagdasarjani*-*T. urticae* interactions were narrower in comparison with that recorded in the first series of experiments (direct effect). It seems that when female *T. urticae* directly interacted with its predator and conspecifics which had affected by predator (first series of experiments), especially *P. persimilis*, it changed its oviposition rate more strictly.

Egg placement and egg aggregation by a mother has mostly investigated in predators and parasitoids who need to avoid kin cannibalism (Lopez-Sepulcre, Kokko, 2002; Schausberger, 2005). Faraji et al. (2000) showed that females of *Iphiseius degenerans* produced eggs in clusters (an extreme form of egg aggregation, Schausberger, 2005) and related females deposited eggs closer than the unrelated ones did. Chittenden and Saito (2001) demonstrated that phytoseiid mites with greater number of eggs lay eggs closer to each other. To our knowledge, rare investigations have targeted the egg aggregation in herbivorous mites. Thus our study is of the first providing

evidence that females of *T. urticae* tend to lay eggs in significantly closer distances from each other when they realize the predator (either *P. persimilis* or *T. bagdasarjani*) presence. Interpreting the significant reduced pairwise distances between eggs mostly recorded from the eggs 1–4 and not-significant distances mostly recorded from the latest ones, we need to design new experiments.

Our results showed that when *T. urticae* females received odours related to predator-prey interactions in their oviposition patch, regardless of being affected by predator directly or indirectly (in their preconditioning container), they decreased the pairwise egg distances in at least 4 and at most 6 pairs of eggs, while when odours were absent in the oviposition container, the distances decreased in at least 2 and at most 3 pairs of eggs. Thus it seems important for the ovipositing *T. urticae* to perceive risk at the time of (in coincident with) laying eggs. When *T. urticae* females lay their eggs closer to each other, they reduce their movement activity during oviposition and consequently the female exposure to the predator and the risk of predation would decrease. Little is known about whether the time of risk experience would affect the spider mite oviposition pattern. Zeraatkar, Zahedi Golpayegani and Saboori (2013) discussed the effect of relatedness on egg distances in three samples of *P. persimilis*. They found that when two female predators were introduced to the same patch, the distance of second female eggs from the first ones was not affected by kinship. Chittenden and Saito (2001) reported about the variation in egg-laying patterns between the species of Phytoseiidae and correlated the feeding type and egg distances but, rare documents have reported the variation of oviposition pattern in spider mites or even any herbivorous mite species.

Several studies have demonstrated the effect of prey mite species on the biological aspects of the predators (Dicke, Sabelis, de Jong, 1988; Gnanvossou, Yaninek, Hanna, Dicke, 2003) but to our knowledge, little information has addressed whether the predator species could alter that in spider mites. Hackl and Schausberger (2014) noted delayed and/or decreased oviposition could be of typical antipredator responses of spider mites. Fernández Ferrari and Schausberger (2013) showed that *T. urticae* laid fewer eggs in the presence of cues of *P. persimilis* and *Amblyseius andersoni*, but they did not investigate the probable changes of prey oviposition period in such situations. Our study showed that the oviposition period of *T. urticae* was reduced significantly either in direct predator (*P. persimilis*/ *T. bagdasarjani*) presence or when females received odours related to predator-prey interactions in their preconditioning container, even if the odours were not present in their second container. Although *T. urticae* oviposition period was shorter in the treatments with *P. persimilis* (in comparison with those with *T. bagdasarjani*), this difference was only significant in the direct presence of a predator, when the odours related to predator-prey interactions were present in the oviposition container. Reducing the oviposition period along with less oviposition rate (mentioned previously) could be considered as an adopted strategy to decrease the risk of predation.

Predation could change the behavior, biology and morphological characters of prey individuals. As a response, prey could develop a wide range of adaptations to reduce the risk of predation. It is known that spider mites are able to detect predators by chemical cues they receive (Grostal, Dicke 1999). Here, we showed that such recognition could induce some types of antipredator behaviors, i.e. oviposition rate reduction, manipulating the distances between eggs and reducing the oviposition period. Our results are of rarely published information about the antipredator behaviors of spider mites.



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