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Article

Different forms of *Tetranychus urticae* Koch and their plasticity in retaining eggs in the presence of predatory mites, *Amblyseius swirskii* and *Phytoseiulus persimilis*

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Abstract

Recent reports indicate that female prey species may increase the time to oviposition in order to prevent egg predation. The generality of this behavior is unknown especially among herbivorous mites. We used females of two forms of *Tetranychus urticae*, red and green forms, to study whether they retain eggs in response to exposure to the predatory mites *Phytoseiulus persimilis* and *Amblyseius swirskii.* Females were tested in two situations: 1) receiving cues related to predator-prey interaction; 2) perceiving the direct presence of predator. None of the treatments induced the *T. urticae* forms to retain eggs. The egg development time of the green form was significantly shorter than that of the red form after receiving cues related to *P. persimilis*-prey interactions. The egg development time of the forms did not show significant difference in the direct presence of each of the predator species. The probability of hatching plasticity in *T. urticae* is discussed.

Key words: Egg retention; hatching plasticity; oviposition; Phytoseiidae; spider mites.

Introduction

Parental care defined as "parental behavior that increase the fitness of the offspring" (Suzuki 2013), has evolved in many lineages of invertebrates in diverse form of cares (Trumbo 2012). In insects, females often care for their offspring, although some rare paternal cares have also been reported (Tallamy 1994). Biparental care has evolved in insects (Blattodea, Coleoptera, and Hymenoptera) and is mostly associated with constructing nests and preparing food for young (Trumbo 2012; Suzuki 2013). Parents might obtain both a short term benefit (increasing offspring survivorship) and long term benefits (fitness advantages later in life) (Grafen 1988) through their caring behavior. Predators could prevent prey counterattack on their offspring by putting eggs in an area where prey are not present (Faraji *et al.* 2001). Magalhães *et al.* (2005) showed that predators respond to large-sized prey counterattack by killing young prey. Saito *et al.* (2008) have pointed out that the female spider mites (*Stigmaeopsis* spp.) provided predators with two kinds of nests: void and true ones. The void nests reduced the predator's searching efficiency and deterred the predators inactively. Simpson (1995) found that spiders that protected their young by guarding eggs, produced larger clutches than those genera which did not show guarding behavior.

Protecting eggs is considered as one of the most primitive forms of parental care (Zink 2003). Binckley and William (2002) demonstrated that natural selection favor females that detect correct time and site of oviposition. Adult females should assess the risk of egg predation and pursue a strategy to protect their eggs that are not able to escape from predators (Nomikou *et al*. 2003). Parents might also select an alternative site for oviposition, resorb the egg material for later or retain the eggs inside their body until they find a safe site (Montserrat *et al*. 2007).

Egg retention - individual flexibility in oviposition rate (Montserrat *et al.* 2007) - could be considered as an effective caring method for young in response to the presence of predators. Montserrat *et al*. (2007) were the first who demonstrated that the presence of predators could induce female prey to retain eggs inside their body until they found less risky oviposition sites. They discussed that the development of these eggs would continue inside the female body. They showed eggs that were laid by the predatory mite, *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) females in the presence of phytoseiid predator, *Iphiseius degenerans* (Berlese) hatched earlier than those laid in the predator's absence.

In this study, we investigated the oviposition behavior of two forms of *Tetranychus urticae* Koch (Acari: Tetranychidae) in response to the presence of their predatory mites *Amblyseius swirskii* and *Phytoseiulus persimilis*. Both *Tetranychus urticae* forms are polyphagous plant mites and key pests that attack vegetables, fruits, crops, cotton and so on throughout the world (Sato *et al*. 2004; Wang *et al*. 2004; Cloyd *et al*. 2009) with a high rate of fecundity and short development time. The predatory mites used in this research were *Amblyseius swirskii* Athias-Henriot and *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae), which are successfully used in *T. urticae* control (Rasmy *et al.* 2004; Nadeali *et al.* 2014). Although several behavioral investigations revealed the oviposition pattern of predatory mites (Zhang *et al.* 1999; Faraji *et al.* 2001; Rahmani *et al*. 2009), very few have focused on herbivorous mites (Moghadasi *et al*., unpublished data). Therefore it was of interest to shed the light on spider mites and find out whether the parental strategy of egg retention would appear in *T. urticae* red and green forms in the presence of *A. swirskii* and *N. californicus*.

Material and methods

Plants and mites

Common bean plants (*Phaseolus vulagaris* L. (Fabaceae) var. Red Alamouti) used in this study were grown in beds under commercial conditions (soil: perlit; 50:50%) in a greenhouse. Bean plants were irrigated daily with tap water and fertilizer solution of NPK (20×20×20) and were kept at controlled conditions (23 ± 1 °C, 16L:8D photoperiod, 65 ± 5% RH) in growth chambers at the Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran. Spider mites, *Tetranychus urticae* (green and red forms separately) were reared on bean plants. Fresh bean plants were added to the rearing system regularly.

The predatory mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius swirskii* were kept on masses of detached bean leaves deposited upside down on a plastic sheet on a water saturated sponge. The plastic sheet was surrounded by napkin tapes (thin napkin bands) that were put into the water from another side so that the predatory mites could drink water.

Egg development time of T. urticae *in the presence of predator cues*

Each experimental arena consisted of a 2 × 2 cm^2 detached bean leaf put upside down on water-saturated sponge contained in a 6 cm diameter Petri dish. A wet napkin tissue (2.1 × 2.1 cm^2) was placed between the leaf and sponge to prevent the mites from escaping and floating in the sponge pores. To test whether cues related to the predatory mites (*A. swirskii* / *P. persimilis*) would decrease the egg development period of spider mites, a single female predatory mite and five same-aged *T. urticae* mated females were put on leaf discs in Petri dishes which afterwards considered as treatment. After 24 hours, the survived spider mites (and their eggs) and the predator were removed from the discs, but the predator related cues (eggs and feces and prey cadavers), were not. Control leaf discs were set up like the treatment discs, however predators were not added. One new *T. urticae* female (that had not been exposed to predators) (green/red form) was added into each (treatment/control) leaf disc. According to the pre-tests, eggs began to hatch after 72 h of development. Therefore we monitored our experimental leaf discs every 15 minutes after the first egg hatched and continued checking the eggs every 15 minutes for 10 hours, so that we could record the exact time of oviposition for each egg. The time of larvae emergence was recorded until the last egg hatched. This experiment was replicated 20 times for each of the green and red form of *T. urticae*, separately. All the replicates of each treatment were setup on the same experimental date. Data analysis was performed by two independent t-test through SPSS 19.

Egg development time of T. urticae *in response to the predator presence*

The experimental arenas consisted of Petri dishes setup exactly the same as described above for the previous experiment. Six same-aged mated *T. urticae* females (green/red form) and two same-aged predator females (*A. swirskii* / *P. persimilis*) were added to the leaf discs. Petri dishes without predators (contained only six *T. urticae* females) were considered as Control. After 24 hours, the predators and their cues (eggs, faeces) and also *T. urticae* cues were removed from the treatment leaf discs. The Control discs were also excluded from spider mite cues (survived *T. urticae* females were kept in both treatment and Control Petri dishes. Leaf discs were monitored every 15 minutes for 6 hours, so that we could record the exact time of oviposition for each egg. The time of larval emergence was recorded until the last egg hatched. This experiment was replicated 20 times for each of the green and red form of *T. urticae*, separately. Data analysis was performed by two independent t-test through SPSS 19.

Results

Egg development time of T. urticae *in the presence of predator cues*

When *T. urticae* females oviposited on leaf discs containing predator cues and conspecific killed bodies, their eggs did not hatch significantly earlier than those laid by females in absence of predators (Table 1). When *A. swirskii* was used as a predator, 83% of *T. urticae* red form eggs and 38% of those related to green form hatched within three hours of each other (since the first hatching was recorded), while in the presence of cues related to *P. persimilis*, the fraction of eggs hatched in this period was recorded as 60% and 77% for the red and green forms, respectively.

Table1. Independent t-test for comparing the egg development time (hours) of *T. urticae* (green /red

form) when perceived cues related to *P. persimilis* or *A. swirskii* (treatment) with Control.

Predator species	Source of variation	egg development time (green form)	d*f*	P value	egg development time (red form)	d*f*	P value
P. persimilis	Treatment	91.27 ± 0.63	29	0.337*n.s*	95.83 ± 1.02	26	0.377*n.s*
	Control	92.76 ± 1.75	15.1		97.26 ± 1.24	24.15	
A. swirskii	Treatment	98.23 ± 0.83	27	0.408 *n.s*	90.55 ± 0.627	33	0.408*n.s*
	Control	97.53 ± 0.5	20.1		91.41 ±0.81	30.52	

n.s. = not significant, each P. value is considered for the difference between the mean development time related to the Control and treatment of the same predator species.

Comparing the development times of *T. urticae* red and green forms when perceived no predator cues (controls) no significant difference was observed (independent t-test, P = 0.069, df = 24). The egg development time of *T. urticae* red form was significantly longer (P < 0.01) (Table 2) than that for green form when they perceived cues related to *P. persimilis.* As the independent t-test showed a significant difference (P < 0.05) between egg development times (Controls) of *T. urticae* red and green forms before receiving cues related to *A. swirskii*, we did not compare their development times when received cues related to *A. swirskii*.

Table 2. Independent t-test for comparing the egg development time (hours) of *T. urticae* green and red forms when perceived cues related to *P. persimilis*

Predator species	*T. urticae* form	*T. urticae* egg development time (hours)	P value
P. persimilis	Green	91.27 ± 0.63	0.001**
	Red	95.83 ± 1.02	

** = P < 0.01

Egg development time of T. urticae *in response to the predator presence*

When *T. urticae* females oviposited on bean leaves in the presence of predators, their eggs did not hatch significantly earlier than those laid by females exposed no predators (Table 3). When *A. swirskii* was used a predator, 57% of *T. urticae* red form eggs and 28% of those related to green form were hatched within three hours of each other (since the first hatching was recorded), while in the presence of cues related to *P. persimilis*, the fraction of eggs hatched in this period was recorded as 38% and 10% for the red and green forms, respectively.

Table 3. Independent t-test for comparing the egg development time (hours) of *T. urticae* (green / red form) when perceived the direct presence of *P. persimilis* or *A. swirskii* (treatment) with Control

Predator species	Source of variation	egg development time (green form)	d*f*	P value	Egg development time(red form)	d*f*	P value
P. persimilis	Treatment	79.48 ± 1.03	38	0.359 *n.s*	80.95 ± 1.35	31	0.624 *n.s*
	Control	78.24 ± 0.84	36		80.24 ± 0.745	19.38	
A. swirskii	Treatment	80.25 ± 1.44	32	0.999 *n.s*	76.9 ± 1.42	26	0.148 *n.s*
	Control	80.25 ± 0.78	20.57		79.72 ± 1.24	25.5	

n.s.= not significant, Each P. value is considered for the difference between the mean development time related to the control and treatment of the same predator species.

Comparing the development times of *T. urticae* red and green forms in the absence of the predator (Controls) no significant difference was observed (*P. persimilis*: P = 0.08, *A. swirskii*: P = 0.706). The egg development time of the *T. urticae* green form did not differ with that in the red form neither in the presence of *P. persimilis* , nor in the presence of *A. swirskii* (P > 0.05) (Table 4).

Table 4. Independent t-test for comparing the egg development time (hours) of *T. urticae* green and red form when perceived the direct presence of (a) *P. persimilis* or (b) *A. swirskii*

Predator species	*T. urticae* form	*T. urticae* egg development time (hours)	P value
P. persimilis	Green	79.48 ± 1.03	0.391 *n.s*
	Red	80.95 ± 1.35	
A. swirskii	Green	80.25 ± 1.44	0.111 *n.s*
	Red	76.9 ± 1.42	

n.s. = not significant

Discussion

Egg development time of T. urticae in the presence of predator cues

Prey can take care of their offspring using a variety of methods, *i.e.* depositing eggs away from risky patches, delaying oviposition, killing juvenile predators, and retaining eggs as studied here. Our results showed that when *T. urticae* females (without any previous experience with predator) were inserted in a patch with a predator (*P. persimilis* / *A. swirskii*) cues, *i.e.* eggs and faeces (direct cues), alarm pheromone of conspecifics (indirect cues) and also the smell of their killed bodies, neither the red form nor the green form had retained the eggs inside their bodies. Effect sizes were small and statistical power was insufficient to declare differences between the treatment and Control groups (Table 1). According to Montserrat *et al.* (2007), when eggs are retained, they are older at the time of oviposition so that they are expected to hatch earlier in comparison with the ones with normal development procedure. Here, although both *P. persimilis* and *A. swirskii* posed a high predation risk for spider mites (killing eggs and juveniles), their presence could not elicit egg retention (keeping eggs inside the body) neither in the green nor in the red form of *T. urticae*. We did not record the oviposition rate of *T. urticae* different forms here, but Moghaddasi *et al.* (unpublished data) recorded a significant reduction in the oviposition rate of *T. urticae* green form in the presence of *P. persimilis* and *N. bagdasarjani* which was interpreted as a kind of maternal care in prey.

Our results revealed that *T. urticae* females had not retained eggs inside their body in the risky situation provided with, thus we focused on *T. urticae* probable hatching plasticity. For many predators, prey embryos are of major attraction despite their few options for reducing the risk of being killed. When prey hatchlings encountered with a high risk of mortality, the eggs (embryos) would favor a delay in hatching, while when the mortality risk increased for eggs, they favor earlier hatching (Chivers *et al.* 2001; Anderson and Brown 2009; Kusch and Chivers 2004). Considering that amphibians have provided a model system for studying the effects of predation on metamorphosis (Chivers *et al.* 2001), we can find similarity between our results and Anderson and Petranka (2003) who demonstrated that despite the potential benefits of altering the hatch time, the embryos of the wood frog, *Rana sylvatica* LeConte, did not respond to their predatory odonate, *Anax junius* Drury. Peralta Quesada and Schausberger (2012) have provided an exclusive evidence on prenatal chemosensory learning in *N. californicus* and its consequences on the predator postnatal foraging behavior (the only published document about arthropods) but they did not discuss whether this learning ability would also affect the embryos hatching procedure. If we focus on the functional sensory receptors of embryos that assist their behavioral reactions, we can conclude that either the absence of such apparatus has impeded the embryos from hatching at an optimal (sooner) time, or the cues were insufficient for the embryos to explore such a response.

According to our observations, in the presence of *cues* related to *P. persimilis* and the spider mite killed bodies, the egg development time of *T. urticae* green form was significantly shorter than that in the red form ($P < 0.01$) (Table 2). Abd El-Wahab and Abouhatab (2014) reported that different forms of *T. urticae* could affect their insect predator attraction behavior differently. Takabayashi *et al.* (2000) suggested that the effect of elicitors of the red and green forms of *T. urticae* differed because different infestation levels of each form led to different *P. persimilis* attraction responses. The infestation area in our research was nearly 5% of the leaf surface [slightly infested according to Takabayashi *et al*. (2000)], while our results showed that *T. urticae* green form had undergone more risk on behalf of *P. persimilis* (less egg incubation time, Table 2) in comparison with the red form, which is in contrast with Takabayashi *et al.* (2000).

Egg development time of T. urticae *in response to the presence of predator*

When *T. urticae* females (green/red form) perceived the predator presence directly for 24 hours, the development time of their eggs did not show a significant difference (although small reduction) comparing with Control. Also, unlike the first experiment (in the presence of predator cues), the egg incubation time of the *T. urticae* forms did not differ significantly in the presence of either *P. persimilis* or *A. swirski.* Our interpretation is that although *T. urticae* exposed to predators directly and for a longer time (in comparison with the first experiment), they were not able to retain eggs inside their body (Table 3). As the eggs had passed their incubation time completely outside the body of mother, comparing the hatching time in the presence and absence of predator indicated no hatching time flexibility in this experiment. This might be due to insufficient alarms received on behalf of predators or lacking the manipulation ability of hatching time in embryos.

Retaining eggs inside the body for decreasing the risk of predators for prey eggs has little been studied. Montserrat *et al.* (2007) were the first who demonstrated that intraguild predatory mites could induce egg retention in intraguild prey. To our knowledge, the present research is the first paper studied the probable ability of a tetranychid prey to retain eggs in the presence of predators or predator cues. Because of its recent discovery in mites, the generality of predator-induced egg retention in herbivorous mites is still confronted with lack of information.

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انعطاف فرم‌های متفاوت ***Tetranychus urticae*** **Koch** در نگهداری تخم‌ها در بدن با حضور کنه‌های شکارگر ***Amblyseius swirskii*** و ***Phytoseiulus persimilis***

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چکیده

پژوهش‌های اخیر نشان می‌دهد که افراد مادهٔ گونه‌های شکار می‌توانند زمان تخم‌گذاری را به منظور پیشگیری از شکارشدن تخم‌ها به تعویق اندازند. این‌که چنین رفتاری تا چه میزان عمومیت دارد –به‌ویژه در میان گیاه‌خواران– امری ناشناخته است. در این پژوهش افراد ماده دو فرم سبز و قرمز کنه تارتن *Tetranychus urticae* را از بابت امکان نگهداری تخم‌ها در بدن در مواجهه با کنه‌های شکارگر *Phytoseiulus persimilis* و *Amblyseius swirskii* بررسی شد. کنه‌های مادهٔ تارتن در دوحالت آزموده شدند: ۱) با دریافت نشانه‌های شیمیایی متعلق به برهم‌کنش شکار–شکارگر؛ ۲) در حضور مستقیم شکارگر. کنه‌های تارتن در هیچ‌کدام از تیمارها، تخم‌ها را در بدن نگه نداشتند. پس از دریافت نشانه‌های شیمیایی مربوط به برهم‌کنش شکار–شکارگر، دورهٔ رشدی تخم‌های کنه تارتن فرم سبز، به‌طور معنی‌داری کوتاه‌تر از دوره رشدی تخم‌های کنه تارتن فرم قرمز بود. در حضور مستقیم شکارگر، دوره رشدی تخم در فرم‌ها باهم تفاوت معنی‌داری نشان نداد. در مورد احتمال انعطاف تفریخ در *T. urticae* بحث شد.

واژگان کلیدی: نگهداری تخم؛ انعطاف در تفریخ؛ تخم‌گذاری؛ Phytoseiidae ؛کنه‌های تارتن.

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