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**Article**

# *Tetranychus urticae* (Acari: Tetranychidae) male defensive behavior against *Phytoseiulus persimilis* (Acari: Phytoseiidae)

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**ABSTRACT**
The nature of spider mite counterattack and defensive behavior and their effects on predatory mites have only been investigated in social species. Here, we have examined the defensive success of *Tetranychus urticae* Koch (Acari: Tetranychidae) male individuals in the presence of *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) juveniles. We recorded the number of *T. urticae* eggs eaten (killed) within three days along with monitoring the predator (dead/alive) status. The defensive behavior of *T. urticae* male was considered as success when the predator had consumed less than 50% of the prey eggs and was killed at the end of the experimental period. Our main hypothesis was that introducing an additional male would increase the defensive success rate. Results showed that the success rate was significantly higher in the patches with two *T. urticae* male individuals compared to one. No significant difference were observed among the egg-eating (killing) rate within the three consecutive days of experiment in patches with one male, while in the treatments with an additional male, the egg killing rate of the third day was significantly higher than that on the first day. We also hypothesized that male *T. urticae* with significant higher rate of defensive success should be morphologically different in comparison with the defeated ones. We found no significant differences in the length of chelicera, first leg and body (length and width) between the successful versus defeated males. We concluded that *T. urticae* can attack the predator, but the weapon by which the success happens remained unclear.

**KEY WORDS:** Behavior; defensive; interaction; predation; spider mite.

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## INTRODUCTION

The life-dinner principle as an asymmetric selection pressure suggested that prey should escape alive from interactions with its predator using a stronger selection rather than predator (Dawkins and Krebs 1979; Humphreys and Ruxton 2020). The Dicy-Dinner Dilemma as a novel alternative model considered a broader range of circumstances and focused on differentiating between the times that prey escaped because of the predator declining to chase, and the cases when the predator was unable to chase the prey (Humphreys and Ruxton 2020). According to both models, avoiding predation is a crucial challenge for prey in arthropod predator-prey systems (Saito and Zhang 2017). Besides, the usual size difference between the predator (large) and prey (small) might increase the capture success rate of prey (Magalhães *et al*. 2005), but ontogenetic size overlap would lead to

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role reversal, so that the prey attacks and the predator defends (Palomares and Caro 1999; Magalhães *et al*. 2005). Several examples of such role reversals have been demonstrated. Janssen *et al*. (2002) showed that *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) larvae killed significantly more eggs of its dangerous [*Iphiseius degenerans* (Berlese) (Acari: Phytoseiidae)] than its harmless predator [*Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae)]. Choh *et al*. (2012) showed that *I. degenerans* juveniles exposed to their adult predator ([*Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae)], would lead to their anti-predator behavior as an adult in form of killing *N. cucumeris* juveniles. Choh *et al*. (2014) demonstrated that witnessing the killing of juveniles by *N. cucumeris*, induced adult females of *I. degenerans* to kill their heterospecific juveniles at a faster rate. Faraji *et al.* (2001) reported that female *I. degenerans* showed a flexible antipredator behavior when their counterattacking prey (i.e. *F. occidentalis*) is present.

In spider mites (Acari: Tetranychidae), counterattack behavior has just been manifested in a few subsocial species. Yano *et al*. (2011) reported a variation in the counterattack and defensive success rate of the social species *Stigmaeopsis miscanthi* (Saito) different forms against *Typhlodromus bambusae* Ehara larvae. Saito and Zhang (2017) suggested that the social spider mite, *Stigmaeopsis nanjingensis* (Ma & Yuan) (Acari: Tetranychidae) could prevent juvenile predators from entering nests using silk webs to lock its predator (*T. bambusae*) youngs out of the nest. Yano *et al*. (2011) demonstrated that the highly aggressive form of *S. miscanthi* showed a stronger tendency than its low aggressive form to kill the predator *T. bambusae*. Saito (1986) studied the biparental counterattack success of *Schizotetranychus celarius* (Banks) (Acari: Tetranychidae) as a eusocial species against *Typhlodromus bambusae* Ehara (Acari: Phytoseiidae) larvae. Ito (2019) indicated a unique mass attacking behavior in *Schizotetranychus brevisetosus* Ehara (Acari: Tetranychidae), which was initiated by female individuals walking outside the nest and followed by larvae and nymphs. Despite relatively common instances of arthropod prey species defending against predators, no investigation has addressed this phenomenon with a non-social spider mite. Therefore, a true understanding of the defensive behavior in male *T. urticae* is needed.

*Tetranychus urticae* is the most common polyphagous spider mite (Sabelis 1985; Fathipour *et al*. 2006) and feeds on more than 1100 documented plant species (Santamaria *et al*. 2020). After colonizing the host plant, *T. urticae* population increases in number very fast (Sabelis 1985). Their most important enemies, phytoseiid mites, would invade and prey on *T. urticae* colonies and destroy them completely (Dias *et al*. 2016), so the prey should employ strategies to reduce the risk of predation. The antipredator behavioral studies in *T. urticae* have mostly focused on behavior of females i.e. avoiding presence on risky patches (Ferrari and Schausberger 2013; Dittmann and Schausberger 2017), changing the oviposition site (Gyuris *et al*. 2017; Murase *et al*. 2017), aggregation (Dittman and Schausberger 2017), and locking out the predator (Saito and Zhang 2017). To our knowledge, no counterattack (as an antipredator behavior) has yet been addressed in *T. urticae* males. Here, we investigated whether *T. urticae* males could express such a response when exposed to *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) as its specific predator (McMurtry *et al*. 2013). We hypothesized that *T. urticae* male individuals show defensive paternal care towards *P. persimilis* nymphs. Our results showed that the number of killed (predated eggs) would decrease and the predator would also be killed. Besides, we studied whether increasing the number of male individuals (cooperation/aggression) on the same patch would affect the result of defense. The probable effect of male morphological characters i.e. the length of the palp and chelicera and the body length and width, on the defending behavior success/defeat was also evaluated.

## MATERIAL AND METHODS

Common bean plants [[*Phaseolus vulgaris* L. (Fabaceae) var. Red Alamouti] were grown in plastic pots in a greenhouse (soil: perlite; 50: 50%) under controlled conditions (25 ± 5 °C, 16L: 8D photoperiod, 65 ± 5% RH) at the Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran. Plants were daily irrigated with tap water and a fertilizer solution of NPK (20 × 20 × 20). Spider mites, *Tetranychus urticae* (green form; food source for the predatory mites) were reared on bean plants. Fresh bean plants were added to the rearing system regularly.

The predatory mites, *Phytoseiulus persimilis*, species clarified prior to experiments, were reared on masses of detached bean leaves, infested with *T. urticae*, placed upside down on a plastic sheet on a water-saturated sponge. The plastic sheet was surrounded by napkin tapes which were put into the water from the other side so that the predatory mites could drink water. Fresh *T. urticae* infested leaves were added to the rearing system and the old predator-free leaves were removed regularly (Overmeer 1985). The cultures were kept in separate growth chambers under controlled conditions (25 ± 1 °C, 16L: 8D photoperiod, 65 ± 5% RH) in the Acarology laboratory at Jalal Afshar Zoological Museum, Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran.

We prepared 2.5 × 2.5 $cm^2$ bean leaf discs to put upside down on water-saturated sponges in Petri dishes (6 cm in diameter), considered as experimental units. An unmated newly emerged *T. urticae* female was inserted into the patch along with a newly emerged male. Care was taken to choose the mating male and females from the same iso-female line so that their kinship rate would increase. The iso-female lines were established by mated females selected from the base population, so that mating happened between a virgin female and her sons. When 6–8 eggs (according to pre-tests) were oviposited (approximately within 4 days), the female and all active stages except males were removed so that only males and eggs remained on the patch. Care was taken to keep the number of prey eggs fixed at the beginning of each experimental day by adding the number of prey eggs which were eaten on the previous day. Twenty-four hours later, a *P. persimilis* young (approximately 3–4 hours old) protonymph was added to the patch and the experiment was started. We recorded the number of killed (eaten) *T. urticae* eggs and the *P. persimilis* (mostly emerged to adult) state (dead or alive) at the end of the third day. The experiment was replicated 20 times. The defensive type of interaction on behalf of male *T. urticae* was considered either as a “success” when less than 50% of *T. urticae* eggs were consumed and also the predator individuals were killed or as a “defeat” when more than 50% of *T. urticae* eggs were consumed (eaten) and the predator individuals stayed alive respectively. When no *T. urticae* eggs were consumed and *P. persimilis* remained alive, the result of defense was defined as “accident” (Saito *et al*. 2011). The same experimental unit with a predator and no male spider mites was considered as control (n = 15 replicates).

To check whether increasing the number of so-called defending males would affect the rate of success, the experiment was repeated (20 replicates) with *two* same-aged *T. urticae* males (from the same iso-female line) placed into the patch. Only the replicates with definite status of eggs and predators were considered as replicates, so that the ones which either the specimens were escaped or the eggs were damaged during transfer process were eliminated. All male spider mites were removed to separate vials of alcohol 70%. Each vial was labeled with the mite status and its experiment identifications. Measurements were carried out to compare the length of the cheliceral stylets (whole length, non-linear measurement), palps, and body (length, width) in the male specimens which were recorded whether as the “succeeded” or “defeated”. Measurements are given in micrometers (μm) and calculated with an Olympus BX 51 microscope digital camera.

### *Data analysis*

Analyses were carried out using SPSS 21. For defensive status with three related treatments, we used the nonparametric Cochran's Q tests. For those Cochran's Q analyses with significant results, we followed up the test with McNemar post-hoc test to find out which specific group(s) differed from others. We used the nonparametric Wilcoxon signed-rank test to compare the success rates between the experimental units with one and two male individuals. The mean ranks of eaten eggs on three consecutive days of the experiment were compared using Kruskal-Wallis H test. Comparing the rate of eaten eggs within *two* consecutive days in patches with defeated *T. urticae* males, we used a nonparametric Mann-Whitney U test. An independent t test was used to find out whether the successful male morphological characters were statistically different from defeated ones.

## RESULTS

### *Defensive state on behalf of one individual* T. urticae *male*

107 *T. urticae* male individuals were used in the study to examine whether predation rates changed over predator survival. Cochran's Q test determined that when an individual *T. urticae* male was introduced to the patch, there was a statistically significant difference in the proportion of predators that consumed more/less than 50% of prey eggs and remained alive or were killed, $\chi2$ (2) = 24.038, $P < 0.01$, with a mean rank of 2.67 for success, 1.17 for defeat and 2.17 for the accident. The post-hoc McNemar's test determined that the proportion of the predators that killed more than 50% of prey eggs and remained alive was significantly less than those consumed less than 50% of *T. urticae* eggs and found killed, $P < 0.01$, so that the defend was considered as “success”.

### *Defensive state on behalf of two* T. urticae *male individuals*

118 individuals were recruited to take part in the study to examine whether predation rates changed over predator survival. Cochran's Q test determined that when two *T. urticae* male individuals were introduced to the patch, there was a statistically significant difference in the proportion of predators who consumed more/less than 50% of prey eggs and remained alive or were killed, ($\chi2$ (2) = 10.40, $P < 0.01$) with a mean rank of 0.92 for success, 0.46 for defeat and 0.15 for the accident. The post-hoc McNemar's test determined that the proportion of the predators who killed more than 50% of prey eggs and remained alive was significantly less than those who consumed less than 50% of *T. urticae* eggs and found killed, $P < 0.01$, so that the defend was considered as “success”. When there was a single male present on each patch, the predator was excluded at a probability of 0.67 ($Z = -8.06$, $P = 0.00$, for the comparison between control and one male patch). The success rate increased to 0.78 ($Z = -8.\ 718$, $P < 0.01$ for the comparison between control and two males). A significant difference in the success rate between one male and two male patches ($Z = -3.317$, $P = 0.01$) was shown by Wilcoxon Signed Rank test.

Kruskal-Wallis test provided no evidence of a difference between the mean ranks of eaten (consumed) eggs on three consecutive days of the experiment ($\chi2$ (2) = 1.733, $P > 0.05$) for the observations in which one individual *T. urticae* male succeeded in defense. For those successful replicates with two male individuals, we recorded a significant difference in the number of preyed eggs ($\chi2$ (2) = 8.24, $P = 0.017$) with a mean rank of 8.35 for the first day, 12.61 and 19.75 for the second and third days. Dunn (post- hoc) pairwise test showed a significant difference between the percentages of the consumed eggs on the first and the third days of the experiment ($P < 0.05$). a Mann-Whitney U test for the observations on patches with one/ two individual defeated male(s) showed that there was not any significant difference (U = 0/ 7.5, P = 1.21/ 0.16) between the percentage of killed eggs in the first and second days of the experiment.

### *Morphological character variation between the “succeeded” and “defeated” males*

Our results showed no significant differences among the mean (± SE) length of stylets in successful males (122.1 ± 1.7), defeated males (119. 1 ± 2.34) and accidentals (124.8 ± 2.13) ($F = 0.64$, $df = 2$, $P > 0.05$). We recorded no significant difference among the mean (± SE) length of first legs in successful males (273.22 ± 0.11), defeated males (278 ± 0.22) and accidentals (272.67 ± 0.11) ($F = 0.78$, $df = 2$, $P > 0.05$). The mean length of idiosoma did not differ between succeeded males (283.06 ± 8.7) and defeated ones (265. 73 ± 12.74) ($P > 0.05$), neither did the mean width of idiosoma (successful males: 177.90 ± 6.9, defeated ones: 189.70 ± 5.08) ($P > 0.05$).

## DISCUSSION

From the perspective of the present study, it was suggested that *T. urticae* males were able to defend against *P. persimilis* juveniles. This could be detected not only in *T. urticae* first leg stabbing-like behavior on predator juveniles (personal observation), but also in *P. persimilis* rate of killing *T. urticae* eggs and the predator status (dead/alive) at the end of the experiment. Previous studies addressed some non-nutritional mediated maternal effects in *T. urticae* which were declared as manipulation of hatching asynchrony, aggregation, and changing the oviposition pattern (Schausberger and Hoffmann 2008; Clouche *et al*. 2014; Moghadasi *et al*. 2019). Schausberger and Sato (2019) discussed the parental effect of *T. urticae* males through alternative reproductive tactics and showed that fighter-mated mothers produced sons that were more likely to guard in comparison to those of unmated and sneaker-mated mothers, but no direct paternal effect was reported. To our knowledge, this is the first study suggesting such behavior in *T. urticae* males. Our results were consistent with Saito *et al*. (2011) who reported that the tetranychid *S. miscanthi* males were able to effectively defend their nests against *T. bambusae* and *N. womesleyi* (Schicha) either by killing or by driving the predators away. Similarly, Saito (1986) demonstrated that *Schizotetranychus celarius* (Banks) males actively killed *T. bambusae* larvae and succeeded in defending offspring. Mori and Saito (2004) also reported that *S. longus* Saito, 1986 males could show a specific mode of counterattack through chasing the *T. bambusae* (intruder) larvae. The chasing behavior recorded in females was weak. The body length of *P. persimilis* deutonymphs was either similar with, or longer than that in *T. urticae* males (personal observations), so that the significant success rate could only be interpreted as the definite success in prey counterattack.

When the number of males increased to two, the defending success rate increased significantly. This was in contrast with Saito *et al*. (2011) who reported a non-significant difference between the one and two defending success rates in low aggressive form (LW) of *S. miscanthi*. The difference between the results could be due to the species level of aggressiveness. Our results were inconsistent with Saito (2010) who discussed that the counterattack effect did not always correspond with *S. longus* male to male aggression. Similarly, Yano *et al*. (2011) demonstrated that adding an extra male would increase *S. miscanthi* counterattack success. Also, Saito and Takada (2009) discussed that aggressive and cooperative behaviors were not alternatives, but could exist simultaneously in a single individual. Potter *et al*. (1976) described the aggressive behavior of *T. urticae* males before mating females, occasional, with considerable grappling and pushing behavior along with injuries which led to the death of one of the males, while we never recorded such a behavior in our replicates. The pairs of male we introduced to each patch were related to the same iso-female line which might interpret their non-aggressive behavior towards each other.

The foraging efficiency of predatory mites in the presence of counterattacking prey has received limited attention. Choh *et al*. (2017) studied the patch selection and oviposition pattern of *N. californicus*. They pointed out that the interaction among prey species could affect predator behaviors. Our results showed that in patches with one *T. urticae* male, the difference among egg consuming rates in three consecutive days was not significant, which means an identical flow of predation by *P. persimilis*, unlike our expectation (additive flow of predation due to predator adolescence). This is aligned with the success we reported for counterattack behavior above i.e. the predator ate less although it needed more. We did not analyze the duration of time which the predator protonymph needed to develop to deutonymph in patches with one or two *T. urticae* males but our observations suggested its long in the former, defensible due to eating less food. In patches with two *T. urticae* males, the predation rate of *P. persimilis* (deutonymph) on the third day of the experiment was significantly more than that (protonymh) on the first day, which matched the additive flow mentioned above. Although the defending behavior was also recorded as "success" in the presence of two males, it seems that the predator needed to act neither more conservative (than), nor as conservative (as) the situation in which one *T. urticae* male was present, i.e. the *P. persimilis* deutonymph preyed on more eggs in comparison to its protonymphs.

Morphological traits and behavioral decisions are integrated (Carvalho and Mirth 2015). Many environmental conditions could impact an animal's behavior, developmental program, and morphology (Mirth and Shingleton 2012; Carvalho and Mirth 2015). Insect body size and morphology are not considered as rigid characters, therefore plasticity of body size will optimize animal survival in new environmental conditions (Carvalho and Mirth 2015). Saito (1990) demonstrated that the length of male first leg is a weapon factor in mating behaviors in *S. miscanthi* which resembled "Repeated jabbing" observed in *S. longus*. The males thrust out their first pair of legs and repeatedly dashed their bodies against competitors. They discussed that the leg size distribution of winning males deviated towards greater lengths. Potter *et al*. (1976) demonstrated that in tetranychid aggressive interactions (mating process), males spread their first legs and extruded their stylets to attack. To our knowledge, this is the first time that morphological plasticity is studied through spider mite male defending behavior against a predator species. Our results showed that a significant difference was observed neither for the mean length of the first legs nor for the mean length of the stylets between the *T. urticae* male (succeeded and defeated) individuals. This is inconsistent with Sato *et al*. (2019) who reported that alternative (aggressive) phenotypes of male *T. urticae* which are selected for managing to acquire *mating*, did not act aggressively. They also found no statistical differences between territorial and sneaker males, concerning the length of the first legs, stylets, and the body. We found no statistical difference between successful and defeated males concerning the body length and width, in comparison with Potter *et al.* (1976) who showed that *T. urticae* male body size could affect the outcome of the mating combat among the intruders. As far as we know, our report is the first study considering the probability of such a selection in *T. urticae* defending behaviors.

Our study provided an example of defending (counterattack) success in *T. urticae* males against its specific predator, *P. persimilis*. Further investigations are needed to find out whether such a defending success on behalf of males (along with maternal care proven: biparental care) could ascertain a little sparkle of subsociality in this species according to Saito (1986) and Hamilton (1964). We concluded that neither the stylets and the first legs as the combatting male weapons, nor the body width and length affected the defending success rate in *T. urticae* males; therefore, we still do not have a definitive morphological explanation for such a phenomenon. Which morphological characters are responsible for this behavior and does the success rate vary in the presence of other predator species, are questions to be answered through further studies.

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# رفتار دفاعی کنه‌های نر *Tetranychus urticae* (Acari: Tetranychidae) در برابر *Phytoseiulus persimilis* (Acari: Phytoseiidae)

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## چکیده

ماهیت رفتارهای دفاعی و حملۀ متقابل و تأثیر آن‌ها روی کنه‌های شکارگر، تنها در گونه‌های اجتماعی بررسی شده است. در این پژوهش احتمال موفقیت کنه‌های نر *Tetranychus urticae* Koch (Acari: Tetranychidae) در دفاع در برابر کنه‌های جوان *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) بررسی شد. تعداد تخم‌های خورده (کشته) شده *T. urticae* و همین‌طور وضعیت شکارگر (زنده/مرده) در طی سه روز ثبت شد. رفتار دفاعی از جانب کنه‌های نر *T. urticae*، زمانی موفق تلقی می‌شد که شکارگر کمتر از ۵۰ درصد تخم‌های شکار را خورده و در پایان آزمایش کشته شده باشد. فرضیه اصلی این بود که اضافه کردن یک نر دیگر، موجب افزایش احتمال موفقیت می‌شود. نتایج نشان داد که احتمال موفقیت به طور معنی‌داری در لکه‌های دارای دو کنۀ نر *T. urticae* بیشتر از این احتمال در لکه‌های دارای یک کنه نر بود. هیچ تفاوت معنی‌داری درمقایسه میزان خورده (کشته) شدن تخم‌ها بین سه روز پیاپی آزمایش در لکه‌های حاوی یک فرد نر مشاهده نشد، این درحالی است که در لکه‌های حاوی نر اضافی، میزان کشته شدن تخم‌ها به طور معنی‌داری از این میزان در روز نخست بیشتر بود. فرض دیگر این بود که نرهای کنۀ تارتن دو لکه‌ای که میزان موفقیت‌شان به‌طور معنی‌داری بیشتر بود، از نظر ویژگی‌های ریخت‌شناسی با نرهای مغلوب متفاوت باشند. هیچ تفاوت معنی‌داری در طول کلیسر، طول پای یکم و عرض و طول بدن، بین نرهای موفق و مغلوب مشاهده نشد. این نتیجه حاصل شد که *T. urticae* می‌تواند به شکارگر حمله کند، اما سلاحی که به‌واسطه آن پیروزی حاصل می‌شود هنوز شناخته نشده است.

**واژگان کلیدی:** رفتار؛ دفاعی؛ برهم‌کنش؛ شکارگری؛ کنه تارتن.

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