

Article

The effect of mating experience, age and territoriality on the male mating competition in *Phytoseiulus persimilis* and *Neoseiulus californicus* (Acari: Phytoseiidae)

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Abstract

Male competition to fertilize the eggs of females would result in conflicts between the members of one sex and evolution of secondary behavioral and morphological characters. Here, we investigated the effect of previous mating experience, territoriality and age on the male mating combat and precedence in two phytoseiid species; *Phytoseiulus persimilis* and *Neoseiulus californicus*. Our results showed that naïve *P. persimilis* males, which had not experienced mating before the experiment, were mostly the ones who were able to mate with the females first. In *N. californicus*, previous experience did not have any significant effect on the male behavior. Both naïve and experienced males were able to mate females equally. Territoriality had no significant effect on male mating competition, in either *P. persimilis*, or *N. californicus*. We suggested that phytoseiid predatory mites might differ in phenotypical mating behaviors, so that although they actively defended their mating territory, the consequences of their variation in phenotypical mating strategies led to a non-significant territoriality. The effect of age on male competing behavior was remarkable both in *P. persimilis* and *N. californicus*. *P. persimilis* younger males precede the elders in mating with females while in *N. californicus*, the older males were the ones who mated with the females first. The effects of female re-mating opportunity, the male phenotypical behavior, and spermatophore storage on male competing behavior are discussed.

Keywords: Mating, spermatophore, behavior, territory, predatory mites, morphological characters.

Introduction

Predatory mites of the family Phytoseiidae include important natural enemies throughout the world, some of which are able to maintain the populations of spider mites (Acari: Tetranychidae) and eriophyid mites (Acari: Eriophyidae) at low levels (Tsunoda & Amano 2001; Pappas *et al.* 2005). Copulation is required for their egg-laying and some species need to re-mate or mate several times to reach their maximum

reproductive capacity (Hoy 1979; Tsunoda & Amano 2001; Pappas *et al.* 2005). Population sex ratio is biased towards females in the field (Toyoshima & Amano 1998) and affected by the number of ovipositing females in a patch (Sabelis 1991).

Mating is a critical process in phytoseiid populations, although few studies have demonstrated the behaviors from meeting to copulation and the factors affected by the mating behaviors (Tsunoda 1994). Amano & Chant (1978a) have proposed two types of mating behavior in phytoseiid mites and called them "*Amblyseius-Typhlodromus* type" in which the males climbed on the female dorsum during the pre-copulatory period and "*Phytoseiulus* type" in which the male moves directly under the female without any climbing.

Some studies have determined the mating behavior of the phytoseiid mites from different aspects. Pappas *et al.* (2005) provided a detailed description about the mating phases of *Kampimodromus aberrans* Oudemans by continuous observations under a stereomicroscope. Momen (1997) reported the direct relationship between the proportion of the *Cydnodromella negevi* (Swirskii & Amitai), *Typhlodromus atbiasae* Porath & Swirski females with their duration of copulation. Zhang *et al.* (2007) showed that *Neoseiulus cucumeris* (Oudemans) belonged to the group of species that needed repeating mating to reach the maximum reproduction rate of females. Tsunoda & Amano (2001) showed that *Amblyseius womersleyi* Schicha females required multiple matings in order to reach their full reproductive capacity. Enigl & Schausberger (2004) assessed if *Phytoseiulus persimilis* Athias-Henriot avoided close inbreeding through kin recognition. Their results showed that inexperienced virgin females were able to perceive the relatedness degree of their potential mates and preferred unrelated males rather than their brothers. There are some evidences that show close inbreeding may bring about some critical fitness problems such as a strong female-biased sex ratio in *Phytoseiulus persimilis* or eggs of inbred lines failing to hatch (Hamilton 1967). Enigl & Schausberger (2004) showed that *P. persimilis* avoided these negative effects through kin recognition. Their results showed that virgin females accepted unrelated males rather than related ones but the detailed behavior of the mites was not discussed.

Little is known about the effect of previous experience, age, and territory on the mating behavior of arthropods, especially mites. There are contrary results about territoriality in *Heterophrynus longicornis* (Butler) (Arachnida: Amblypygi). Some studies reported that *H. longicornis* is territorial, living singly in burrows at the bases of trees. While others suggest that *H. longicornis* is tolerant to conspecifics (Dias & Machado 2007; Carvalho *et al.* 2012). Male *Allothrombium lerouxi* Moss (Trombididae) showed lek-like behavior in which they defended small spermatophore deposition territories from another male (Moss 1960). Dukas (2006) has discussed that gaining experience could influence the mate choice and mating success of both male and females of fruit flies. Mautz & Sakaluk (2008) investigated the effects of age and previous mating experience on pre- and post-copulatory mate choice in house crickets (*Acheta domesticus* L.). They reported that both female age and mating experience could moderate female selectivity. Moore & Moore (2001) showed that male courtship and mating behavior of *Nauphoeta cinerea* (Olivier) (Dictyoptera: Blaberidae) would not change as a function of female age, but females who were older when they mated produced fewer offspring per clutch in comparison with the females mated young. Sato *et al.* (2013) investigated the male spider mite pre-copulatory behaviors and found three types of males including territorial, sneaker, and opportunistic. They reported that the

territorial and sneaker males guard female teleiochrysales and were easily disturbed by rivals.

Here, we have questioned whether the mating precedence of the predatory mites, *Phytoseiulus persimilis* and *Neoseiulus californicus* would be affected by their male previous experience of mating, male territoriality against conspecifics, and male age.

Material & methods

Host plants & pest mites

Common bean plants [*Phaseolus vulgaris* L. (Fabaceae)] were grown in plastic pots containing perlite. Plants were irrigated every day by tap water and fertilizer solution of NPK (20 × 20 × 20) and were kept in controlled conditions (23 ± 2 °C, complete photoperiod, 60–70% RH) in growth chambers at the Mite Behavior Laboratory, Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran. Spider mites (*Tetranychus urticae* Koch) were reared on bean plants in a separate greenhouse (24 ± 2 °C, complete photoperiod, 65 ± 5% RH). New fresh bean plants were added into the rearing system regularly. The spider mite colony originated from the experimental greenhouse of the acarology laboratory in Jalal Afshar Zoological Museum.

Predatory mites

The predatory mites (*P. persimilis* and *N. californicus*) were reared on detached bean leaves infested with *T. urticae* in the germinator (25 ± 2 °C, 16 L: 8D hours photoperiod and 70 ± 5 % RH). They were kept on several detached bean leaves, placed upside down on a plastic sheet that was 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 predator colonies originated from the experimental greenhouse of the acarology laboratory in Jalal Afshar Zoological Museum.

General experimental conditions

We prepared the predatory mites for the experiments by randomly selecting a mated female from the main predator colony. The mated female started to reproduce for several generations and we were able to produce the iso-female line. Afterwards, we put the adult females on a separate leaf disc for oviposition. After 24 hours adult females were removed and eggs were kept in a growth chamber for four days, when the mites reached the deutonymphal stage. All of the same-aged male or female deutonymphs were placed on a separate Petri dish in order to avoid mating.

Effect of previous mating experience on mating precedence

From each pair of same aged males (*P. persimilis* or *N. californicus*), one was placed on a spider mite-infested bean leaf disc (1.7 × 1.7 cm²) alone and the other in a similar Petri dish with three same aged conspecific female predators from the same iso-female line for 24 hours. Afterwards, both male predators were marked by different colors of watercolor and transferred to a Petri dish of spider mite-infested bean leaf (1.7 × 1.7 cm²) with a same-aged, not previously mated, conspecific female from the same line. We monitored the Petri dishes until the first mating was seen. The time of mating, the predator behaviors during mating, and the status of the male having started mating were recorded. We used 26 and 30 replicates for each treatment.

Effect of territory on mating precedence

Territoriality is a behavior in defense of an area against another individual, primarily of the same species. In this experiment, a single male predator (with no previous experience of mating) was placed into a Petri dish (6 cm in diameter) on a spider mite-infested bean leaf disc ($1.7 \times 1.7 \text{ cm}^2$) for eight hours. A same aged, not previously mated, conspecific female, from the same line, was added onto the same leaf disc for one hour. Care was taken to avoid them from mating. The experiment was started one hour later by introducing another same aged, not previously mated, conspecific male from the same line to the leaf disc. The Petri dishes were monitored until the first mating was seen. The time of mating, the predator behaviors during mating, and the status of the male having started mating were recorded.

Effect of age on mating precedence

In this experiment, two conspecific (from one line) males, with 20 hours age difference, that were not previously mated, were marked by different colors of watercolor. They were placed into a Petri dish (6 cm in diameter) on a spider-mite infested bean leaf disc ($1.7 \times 1.7 \text{ cm}^2$) consisting a same aged, not previously mated, conspecific female from the same line. We monitored the mites until the first mating was seen. The time of mating, the predator behaviors during mating, and the status of the male which started mating were recorded.

All experiments were performed under controlled conditions ($25 \pm 2 \text{ }^\circ\text{C}$, 16L: 8D hours photoperiod and $70 \pm 5 \text{ \% RH}$). Data was analyzed through non-parametric binomial - exact test of statistical significance of deviations from expected distribution of observations in two categories - test in SPSS19.

Results

Effect of P. persimilis mating experience on its mating precedence

The first *P. persimilis* males that mated with the females (24 individuals vs. 6 individuals), significant to the male group which had not experienced mating previously ($P < 0.01$) (Table 1).

The average duration of copulation was estimated as $142.25 \pm 11.31 \text{ min}$.

Table 1. The values of binomial test to compare the male mating precedence with and without previous mating experience in *P. persimilis*

Mating precedence	Category	N	Observed Prop.	Test Prop.	Asymp. Sig. (2-tailed)
with no previous experience	1.00	24	0.80	0.50	0.001 ^a
with previous experience	0.00	6	0.43		
Total		30	1.00		

a. Based on Z Approximation.

Effect of N. californicus mating experience on its mating precedence

No significant difference was observed between the number of first males (17 individuals vs. 13 individuals) (with or without previous experience of mating) that started mating with the females ($P > 0.05$) (Table 2).

The average duration of copulation was estimated as $165.44 \pm 9.08 \text{ min}$.

Table 2. The values of binomial test to compare the male mating precedence with and without previous mating experience in *N. californicus*

Mating precedence	Category	N	Observed Prop.	Test Prop.	Asymp. Sig. (2-tailed)
with no previous experience	1.00	17	0.57	0.50	0.585 ^a
with previous experience	0.00	13	0.43		
Total		30	1.00		

a. Based on Z Approximation.

Effect of P. persimilis territoriality on its mating precedence

When the second group of male individuals were introduced to the leaf discs, in which another male individual had found its own mate before, no significant difference was observed between the number of first males (19 individuals vs. 11 individuals) (introduced either sooner or later) that started mating with the females. ($P > 0.05$).

The average duration of copulation was estimated as 118.67 ± 9.16 min.

Table 3. The values of binomial test to compare the male (related to the same or other territory) mating precedence in *P. persimilis*

Mating precedence	Category	N	Observed Prop.	Test Prop.	Asymp. Sig. (2-tailed)
Territorial	1.00	19	0.63	0.50	0.200 ^a
Non-territorial	0.00	11	0.37		
Total		30	1.00		

a. Based on Z Approximation.

Effect of N. californicus territoriality on its mating precedence

When the second male individuals were introduced to the leaf discs in which another male individual had found its own mate before, no significant difference was observed between the number of first males (19 individuals vs. 11 individuals) (introduced either sooner or later) started mating with the females ($P > 0.05$) (Table 4).

The average duration of copulation was estimated as 194 ± 11.52 min.

Table 4. The values of binomial test to compare the male (related to the same or other territory) mating in *N. californicus*

Mating precedence	Category	N	Observed Prop.	Test Prop.	Asymp. Sig. (2-tailed)
Territorial	1.00	14	0.50		1.000 ^a
Non-territorial	0.00	16	0.50	0.50	
Total		30	1.00		

a. Based on Z Approximation.

Effect of P. persimilis age on its mating precedence

When the *P. persimilis* males with different ages were introduced to the leaf discs containing a female from the same line, the first males that had mated with the females, were significant (21 individuals vs. 9 individuals) to the male group which were 20 hours younger than the other group ($P < 0.05$) (Table 5).

The average duration of copulation was estimated as 111.14 ± 7.35 min.

Table 5. The values of binomial test to compare the male mating precedence with considering age in *P. persimilis*

Mating precedence	Category	N	Observed Prop.	Test Prop.	Asymp. Sig. (2-tailed)
Younger	1.00	21	0.70	0.50	0.043 ^a
Older	0.00	9	0.30		
Total		30	1.00		

a. Based on Z Approximation.

Effect of N. californicus age on its mating precedence

When the *N. californicus* males with different ages were introduced to the leaf discs containing a female from the same line, the first males which mated with the females, were significant (21 individuals vs. 9 individuals) to the male group which were 20 hours older than the other group ($P < 0.05$) (Table 6).

The average duration of copulation was estimated as 204.27 ± 9.15 min.

Table 6. The values of binomial test to compare the male mating precedence with considering age in *N. californicus*

Mating precedence	Category	N	Observed Prop.	Test Prop.	Asymp. Sig. (2-tailed)
Younger	0.00	9	0.30		0.043 ^a
Older	1.00	21	0.70	0.50	
Total		30	1.00		

a. Based on Z Approximation.

Discussion

Mating experience

Our results showed that *P. persimilis* males which had not previously experienced mating were significantly the dominant rivals in comparison with the experienced males through the precedence competition. Previous experience did not affect the male competition behavior in *N. californicus*. Relatively few studies have provided detailed information on the mating behavior of mites. Hebets (2003) noted that experience during pre-reproductive life stages of wolf spiders may have a strong impact on their adult mating behavior. He showed that sub-adult females that were exposed to courting adult males, not only mated more frequently with males of their familiar phenotype, but also mostly cannibalized the males of unfamiliar phenotype. Our findings about *P. persimilis* were in contrast to Teal *et al.* (2000), who indicated that prior mating experience in Caribbean fruit flies [*Anastrepha suspense* (Loew) (Diptera: Tephritidae)] could influence the male's ability positively so that they could attract, court, and mate successfully with females. They showed that previously mated males needed less time to initiate mating because males became more sexually aggressive. The authors argued that an endogenous difference such as amount of sexual pheromone (mated males releases at least twice as much pheromones as did the same-aged virgins) could bring about such a behavioral difference. Shakeel *et al.* (2010) studied the mating behavior of the European leafminer [*Saptomyza flava* (Fallén) (Diptera: Drosophilidae)] and noted that although no significant differences were found in pre-courtship, courtship, and mating periods between virgin and once-mated males, the mated males were significantly more likely to mate with females successfully. Cook (1994) also reported that as the number of previous matings in *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) increased, the experienced males directed more mating attempts at

females compared with the virgin males. In our study, not only were there no significant male aggression in *N. californicus*, but *P. persimilis* experienced males were less aggressive in mating competition compared to the naïve ones. Possibly, *P. persimilis* males that have once copulated with females and fertilized their ejaculates successfully, are less enthusiastic to re-mate.

Territoriality

Sokolovska *et al.* (2000) showed that the effect of body size was significant in all fitness components of odonate territorial species. Resende & De Marco (2008) studied the territorial characteristics of some species of the family Libellulidae (Anisoptera) and noted that aggressive attacks among males were common and a clear distinction among the territories was observed. There is little information about the effect of territory on the interacting behaviors among male mites. Here, territory affected the mating precedence of the predator males neither in *P. persimilis* nor in *N. californicus*. This is in contrast with Moss (1960) who reported that *A. lerouxi* (Trombidiidae) showed lek-like behavior and defended small spermatophore deposition territories from other males. Sato *et al.* (2013) demonstrated that territorial males were one of the mating phenotypes in two spotted spider mites which could be easily found and attacked by intruders in comparison with sneaker and opportunistic males. The authors discussed that young males could phenotypically switch to sneaker behavior in order to have more mating success. Our interpretation for the present results are that there might have been some alternative phenotypes of male mating behaviors in the phytoseiid predatory mites, rather than those used in our experiments (i.e. *T. urticae*). Our behavioral records showed that the territory owner males usually did not leave their position on the female dorsum (personal observations, similar to sneaker male spider mites) so that the male did not lose the mating opportunity. We concluded that there might have been a complex of at least two phenotypical mating males (like the ones in *T. urticae*), some of which successfully mate with their own female (like sneakers) and some of which lose their mating opportunity during fighting off with rivals (like territorials), with a consequent of non-significant final territoriality effect. Sato *et al.* (2013) also discussed that alternative mating males might show some morphological differences such as body size which is not considered in our present research. This alternative reproductive trait has also been reported from some insect families such as Scarabaeidae (Emlen 1997) and some species of mites [i.e. *Rizoglyphus robini* Claparède and *Caloglyphus berlessei* (Michael) (Astigmatina: Acaridae)] with fighter and scramble males (Radwan 1993; Smallegange 2011).

Age

Brooks & Kemp (2001) discussed that female preference to mating, with respect to their mate age, could differ among species. Jones *et al.* (2000) reported that some species prefer the middle-aged males to mate with. In the present study, *P. persimilis* younger males out competed the elders in mating precedence, while in *N. californicus*, older males that could transfer more spermatophores (Radwan 1997) acted more aggressively. The mating females in our study were virgin and could not affect their re-mating decision on the age of their new partners (Zofia *et al.* 2012). Also, as neither males had any chance to present their spermatophores to other females prior to the experiment. *Neoseiulus californicus* male behavior was not surprising because of the high density of stored spermatophores in their body. Our interpretation for *P. persimilis*,

where younger males precede the elders, is that younger males might often act as sneakers (similar to *T. urticae*, Sato *et al.* 2013) so that they are more likely to protect their mounted position in comparison with the elders. Our results are in contrast with Savalli & Fox (1998) who discussed that the male age could not influence its mating success in the seed beetle, *Callosobruchus maculatus* (Fabricius) (Coleoptera: Chrysomelidae). While Bergman *et al.* (2011) demonstrated the strong effect of age on the mating behavior of the virgin *Pararge aegeria* (L.) (Lepidoptera: Nymphalidae) females. Prokop *et al.* (2007) also studied whether male age in *Rhizoglyphus robini* could affect its progeny fitness. The authors found that older males were less likely to mate within an hour of pairing. Pervez *et al.* (2004) showed that male age could positively affect the egg viability in a predatory ladybird. Zhang *et al.* (2007) demonstrated that age status of *N. cucumeris* males did not have a significant effect on the reproductive rate of females during the oviposition period. Most studies on mating behaviors of phytoseiids concern female age and its effect on reproduction (Amano & Chant 1978a; Momen 1994; Zhang *et al.* 2007). The effect of male age on its mating precedence and behavior is still unknown in many mite taxa (i.e. the family Phytoseiidae). Brooks & Kemp (2001) demonstrated that female preference with respect to male age could differ among species. Jones *et al.* (2000) also noted that some species showed preference to middle-aged males, but there is little evidence about the effect of male age on their mating competition for female. Radwan *et al.* (2005) showed that older males of *R. robini* lost sperm competition with younger ones (unlike the present study) so that polyandry in this species could be an adaptation to avoid fertilization by the sperm of older males (Radwan 2003). The authors discussed that in *R. robini*, the higher paternity rate of younger males might be due to their better sperm competition. Amano & Chant (1978b) studied the factors affected the reproduction of *P. persimilis* and *Amblyseius andersoni* (Chant) (Phytoseiidae) and reported that in both species the males continued to mate even after they had lost the ability to inseminate the females.

The findings reported here could be an important starting step for further development of behavior-based mating strategies in *P. persimilis* and *N. californicus*. Many questions still remain regarding the effect of age, territory, and experience on the mating behavior of the phytoseiid predators which can be answered by future studies. It also needs to be investigated whether intersexual selection and female choice could affect the male competing behavior.

Acknowledgements

The authors would like to acknowledge the financial support of University of Tehran for this research under grant number 05.6.73149051.

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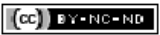
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Received: 25 July 2014

Accepted: 15 December 2014

Published: 15 January 2015

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تأثیر تجربه جفت‌گیری، سن و قلمروگرایی بر رقابت نرها بر سر جفت‌گیری در گونه‌های *Neoseiulus californicus* (Acari: *Phytoseiulus persimilis* و *Phytoseiidae*)

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چکیده

رقابت نرها برای تلقیح تخم‌های افراد ماده موجب بروز کشمکش‌هایی بین افراد هم‌جنس و شکل‌گیری ویژگی‌های ثانویه ریخت‌شناسی و رفتاری می‌شود. در این پژوهش، تأثیر تجربه جفت‌گیری پیشین، قلمروگرایی، و سن بر پیکار و برتری‌جویی کنه‌های نر بر سر جفت‌گیری در دو گونه کنه فیتوزئید شامل *Neoseiulus californicus* و *Phytoseiulus persimilis* بررسی شد. نتایج نشان داد که کنه‌های نر بی‌تجربه *P. persimilis* که پیش از انجام آزمون، جفت‌گیری نکرده بودند، بیشترین افرادی را تشکیل می‌دادند که نخستین جفت‌گیری را با کنه‌های ماده انجام دادند. در *N. californicus* تجربه جفت‌گیری پیشین، هیچ تأثیر معنی‌داری بر رفتار کنه نر نداشت. هر دو کنه نر بی‌تجربه و باتجربه به‌طور برابر با کنه‌های ماده جفت‌گیری کردند. قلمروگرایی تأثیر معنی‌داری بر رقابت نرها بر سر جفت‌گیری در *P. persimilis* و *N. californicus* نداشت. به‌نظر می‌رسد کنه‌های شکارگر فیتوزئید از نظر رفتارهای فنوتیپیک جفت‌گیری متفاوتند، بنابراین باوجودی که به‌طور فعال از قلمروی جفت‌گیری خود محافظت می‌کنند، عواقب ناشی از راهبردهای فنوتیپیک‌شان در جفت‌گیری، منجر به کم‌رنگ‌شدن قلمروگرایی‌شان می‌شود. تأثیر سن بر رفتار رقابت نرها هم در *P. persimilis* و هم در *N. californicus* معنی‌دار بود. کنه‌های نر جوان‌تر *P. persimilis* از نرهای مسن‌ترشان در انجام نخستین جفت‌گیری با ماده‌ها پیشی گرفتند، درحالی‌که در *N. californicus* بیشتر، کنه‌های نر مسن موفق شدند تا برای نخستین بار با ماده‌ها جفت‌گیری کنند. احتمال جفت‌گیری دوباره با ماده‌ها،

رفتارهای فنوتیپیک نرها و ذخیره اسپرمتوفور در آنها و تأثیرشان در رقابت بین نرها مورد بحث قرار گرفته است.

واژگان کلیدی: جفت‌گیری، اسپرمتوفور، رفتار، قلمرو، کنه‌های شکارگر، ویژگی‌های ریخت‌شناسی.

تاریخ دریافت: ۱۳۹۳/۴/۴

تاریخ پذیرش: ۱۳۹۳/۹/۲۵

تاریخ چاپ: ۱۳۹۳/۱۰/۲۵