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Article

Impact of feeding experiences on oviposition and sex allocation of *Neoseiulus californicus* (Acari: Phytoseiidae)

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Abstract

Feeding experiences of predators during immature and adult stages may impact females' reproduction. In the present study, we investigated reproductive performances of *Neoseiulus californicus* when both parents had different feeding experiences on *Tetranychus urticae* and *Frankliniella occidentalis*. Female and male immatures fed on either prey species. Each newly emerged female adult individually mated with a male had either the same or different feeding experience. Prey for mated females were either same as or different from that consumed during their immature stages. Therefore, eight reproductive treatments were created. The highest cumulative fecundity (57.5±3.3 eggs/female) was observed when both female and male fed on *T. urticae* with the lowest fecundity (34.2±2.7 eggs/female) observed when the parents fed on *F. occidentalis.* Daily fecundity and oviposition duration were mainly affected by prey of mated females. Mated females preyed on *T. urticae* had 56.6% higher daily fecundity and 22.3% shorter oviposition duration than those preyed on *F. occidentalis*. No significant difference in offspring sex ratio and egg hatch rate was detected between treatments. About 88% of the first-laid eggs developed to males. Impact of prey species consumed by male immatures was only observed on pre-oviposition duration. The average pre-oviposition duration of females who mated with males fed on *T. urticae* in their immaturity was 33.0% shorter than those females who mated with males fed on *F. occidentalis* in their immaturity. Results of the present study are valuable in optimizing *N. californicus* field release strategies, and will help further investigations into the nutritional requirements of this species.

Key words: reproduction, nutrition history, predatory mites, *Tetranychus urticae*, *Frankliniella occidentalis*

Introduction

Phytoseiid predatory mites are important natural enemies of small arthropods, such as spider mites (Escudero *et al.* 2005; Badrbani *et al.* 2015), gall mites (Castagnoli *et al.* 2003), thrips (Calvo *et al.* 2011), and whiteflies (Seiedy *et al.* 2016), and could also complete their life cycle on pollens (Khanamani *et al.* 2017; Pascua *et al.* 2020). McMurtry & Croft (1997) and McMurtry *et al.* (2013) divided phytoseiid mites into four categories based on their life styles: specialized predators of *Tetranychus* species (type I), selective predators of tetranychid mites (type II), generalist predators (type III), and specialized pollen feeders (type IV). Generally, the first two categories are considered as specialist predators, while the latter two as generalist predators. Phytoseiid mites have a special reproductive method that female mites will not lay eggs if they do not mate (Amano & Chant 1978; Xu & Liang 1994; Hoy 1985, 2009), and all offspring developed from a zygote. The female is diploid and the male is haploid. Haploid male mites also develop from fertilized eggs, in which half of chromosomes were lost or heterogenized and occur 24–48 hours after egg laying (Nelson-Rees *et al.*

1980). This special reproductive mode of phytoseiid mites is called as Pseudoarrhenotoky (Hoy 1985; Nagalkerke & Sabelis 1998; Sabelis *et al.* 2002).

Prey species is an important factor that affects reproductive features of phytoseiid mites, such as fecundity and offspring sex ratio, especially in specialist predators (Mesa *et al.* 1990). For example, Escudero & Ferragut (2005) compared the biological features of two predator mites, *Phytoseiulus persimilis* Athias-Henriot (type I) and *Neoseiulus californicus* (McGregor) (type II), with different *Tetranychus* species as prey. They reported that when feed on *T. urticae* Koch, both predator species have >85% higher cumulative fecundity and >20% higher proportion of female offspring than those feed on *T. evansi* Baker & Pritchard. Gotoh *et al.* (2006) also revealed that *N. californicus* adults survive 67.6% longer when preyed on *T. urticae* than on *Panonychus ulmi* Koch. Besides, *Galendromus occidentalis* (Nesbitt) preyed on *Tetranychus pacificus* (McGregor) (1.1±0.3 days) had 31.3% shorter pre-oviposition duration than those fed on *Eotetranychus willamettei* (McGregor) (1.6±1.0 days) (Lara 2007).

Biological control agents are always suggested to be released before pests outbreak for prevention, namely "Predator-in-First' (PIF) (Kumar *et al.* 2015). Phytoseiid mites in that case would easily face insufficient target pests, so forced to choose non-favorite prey. However, the pest species in the field changed dynamically (Kidd *et al.* 2005), when phytoseiid mites live and grow in such a dynamic environment, feeding experiences vary among individuals and life stages. It's necessary to study how different prey species consumed by both males and females, and during immature and adult stages might impact reproduction to ensure if the predatory mites still have good biocontrol efficiency in the complex field of prey.

A few studies investigated details regarding how feeding experience of both sexes affects reproduction (van den Beuken & Smallegange 2018). Yet, it is still not clear whether the prey species fed by adults have more effect on reproduction than those fed by immatures. Whether predator females can compensate the negative impact on reproduction caused by their poor prey quality immature stages? Whether prey of different quality or species fed by males will affect the reproduction of their partners? Answers to these questions will help understand the general biology and physiology and improve the mass rearing of predators.

In the present study, we used *N. californicus* as the target predator, and two prey species, the two-spotted spider mite *T. urticae* and flower thrips *Frankliniella occidentalis* (Pergande) as prey. *N californicus* is a selective predator of tetranychid species, and also can complete its life cycle on early immatures of *F. occidentalis* (Mizobe *et al.* 2005; van Baal *et al.* 2007). Herein we mainly focused on the reproductive performances of predator females affected by the prey species consumed by males and females during immature stages and by female adults during oviposition stage. Results of this study might provide guides to field release and population evaluations of *N. californicus,* and are also beginning steps in investigating male impact in reproduction regulation of phytoseiids.

Materials and Methods

Mite and insect colonies

The mite and thrips populations were maintained in the Lab of Predatory Mites, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China. The *N. californicus* colony was established from individuals collected in Dinghushan Natural Reserve, Guangdong, China in 2010 (Xu *et al.* 2013), and maintained on kidney bean leaves (*Phaseolus vulgaris* L.) seedlings infected with *T. urticae*. The *F. occidentalis* colony was established from individuals collected from cucumbers grown in a greenhouse, Changping, Beijing, China, in 2005, and maintained on fresh kidney bean seedlings. Breeding colonies were maintained and experiments were conducted at 25±1°C, 70±5% RH, 16:8 hours (Light: Dark).

Experimental procedures

Approximately 100 gravid *N. californicus* were randomly collected the colony and placed in a rearing box (17.5 × 17.5 × 7 cm^3) to achieve synchronous eggs. The rearing box has three layers of soaked sponges (13 × 13 × 1.5 cm^3), two layers of filter papers (dia. 9 cm), and a piece of black plastic film (dia. 7 cm) placed in successively from bottom to top, and had a hole (dia. 5 cm) covered with 250 mesh nylon on the lid. Gravid females were fed with sufficient *T. urticae* for 24 h, and about 300 eggs were laid. Eggs were removed using a fine paintbrush and reared individually in rearing units (dia. 1 cm) made of 3 acrylic layers as described in Zhang *et al.* (2015). After egg hatch, half of individuals were fed with mixed stages of *T. urticae*. Another half of individuals were each provided with 20 1st instar nymphs of *F. occidentalis* daily. Prey were placed on a fresh bean leaf disc on the floor of rearing unit. For each treatment, prey amount (>20) exceeded the daily maximum consumption rate of *N. californicus* (Rahmani *et al.* 2009; Song *et al.* 2016)

Sex of newly emerged *N. californicus* adults was examined (McGregor 1954; Xu *et al.* 2013). For each prey treatment, ca. 50 females and 50 males were collected. We set up four mating treatments, i.e., females that fed either on *T. urticae* or on *F. occidentalis* during immature stages mated with males that fed on either prey species. Each pair was placed in a rearing unit and observed until the termination of copulation. As *N. californicus* females that multiply mate in 48 h have maximum fecundity (Gotoh & Tsuchiya 2008), males were allowed to state in the rearing unit for 48 h and removed afterward. The mated females were fed either with the same prey species or with another species afterwards. Therefore, eight reproductive treatments were created: 2 prey of female immatures × 2 prey of male immatures × 2 prey of adult females (Table 1). There were 12 replicates for each reproductive treatment, and the specific replicates was shown in the corresponding table of results.

Mated females were individually introduced into the rearing units and changed into new units daily with eggs kept in the old ones for development. All the females were observed daily until death. The preoviposition, oviposition and post-oviposition duration, daily fecundity and cumulative fecundity, and egg hatch rate were recorded. Predatory mites usually show stable patterns in sex allocation of the first few eggs (Toyoshima & Amano 1998), therefore the first three eggs of each female were also reared separately until they developed to adulthood and adult sex was identified. The short and long diameters of each of these eggs were also measured, and their sizes were estimated using volume formula of prolate spheroids, $V = \frac{4}{3}\pi a^2 b$ (a, b respectively represent the half-diameter of each axis, $a < b$). The remaining eggs of each female were reared together to adult stage, developmental duration from eggs to adults and sex ratio of offspring were recorded.

Statistical analysis

Three-way ANOVAs was used to analyze the impact of prey species consumed by female during immature (F-I) and adult (F-A) stages, and male during immature stage (M-I) on reproductive parameters, including daily fecundity, cumulative fecundity, pre-oviposition duration, oviposition duration, post-oviposition duration, female adult longevity, hatching rate, proportion of female offspring and sex order of first three eggs. Four-way ANOVA was applied to determine the impacts of the above three factors (i.e., F-I, F-A and M-I) and sex of eggs on egg size and offspring developmental duration. Linear regression was performed to describe the relationship between egg size and developmental duration. Due to limited number of replicates, only the impacts of main factors and two-way interactions were examined. Chi-square test was used to compare the pattern in sex allocation of the 1st three eggs. All analyses were conducted using SPSS statistics 22.0 with a rejection level set at $P < 0.05$.

Results

Impact of prey species on reproductive performances of N. californicus

The pre-oviposition, oviposition and post-oviposition duration, and longevity of *N. californicus* were all significantly affected by prey species of female adults (Table 2). When female adults preyed on *F. occidentalis*, their pre-oviposition and oviposition duration, and longevity were 126.5%, 28.6%, and 8.3% longer than that preyed on *T. urticae*, respectively, while post-oviposition duration was 36.0% shorter (Table 3).

TABLE 1. Reproductive treatments depending on the prey species fed by the immature females and males and ovipositing female adults.

Sex and Stage	Prey							
Female immature	Tu	Tu	Fo	Fo	Tu	Tu	Fo	Fo
Male immature	Tu	Fo	Tu	Fo	Tu	Fo	Tu	Fo
Female adult	Tu	Tu	Tu	Tu	Fo	Fo	Fo	Fo
Treatments	I	II	III	IV	V	VI	VII	VIII

Tu, *Tetranychus urticae*; Fo, *Frankliniella occidentalis*.

TABLE 2. Impacts of female immature prey, male immature prey and female adult prey on *Neoseiulus californicus* reproductive performances.

Source	df	P							
		Daily fecundity	Cumulative fecundity	Pre-oviposition duration	Oviposition duration	Post-oviposition duration	Female adult Longevity	Hatching rate	Proportion of Female offspring
F-A	1	**<0.001**	**0.031**	**<0.001**	**<0.001**	0.017	0.112	0.861	0.147
F-I	1	0.698	**0.042**	**0.009**	0.194	0.519	0.844	0.697	0.652
M-I	1	0.583	0.352	**0.002**	0.301	0.332	0.272	0.870	0.884
F-A * F-I	1	0.942	0.966	0.360	0.816	0.061	0.164	0.378	0.724
F-A * M-I	1	0.121	0.794	0.410	0.392	**0.046**	**0.041**	0.716	0.414
F-I * M-I	1	0.617	0.898	0.112	0.448	0.558	0.434	0.706	0.583
Error	71								

F-A, prey species of female adults; F-I, prey species of female immatures; M-I, prey species of male immatures.

Significant impacts of prey species consumed by male or female immatures on pre-oviposition stage were also observed. When both female and male immatures fed *F. occidentalis*, the pre-oviposition duration was the longest (Table 3). Marginal significant impacts of interaction between prey consumed by female adults and male immatures on post-oviposition duration and female longevity were also detected (Figure 1).

Daily and cumulative fecundity were also significantly affected by female adult prey (Table 2). When female adults preyed on *T. urticae*, the daily and cumulative fecundity were 54.7% and 26.1% higher than those preyed on *F. occidentalis*, respectively. In addition, females preyed on *T. urticae* during immature stages also had higher fecundity than those preyed on *F. occidentalis*. No significant impact of prey on egg hatch rate and sex ratio was observed (Table 2).

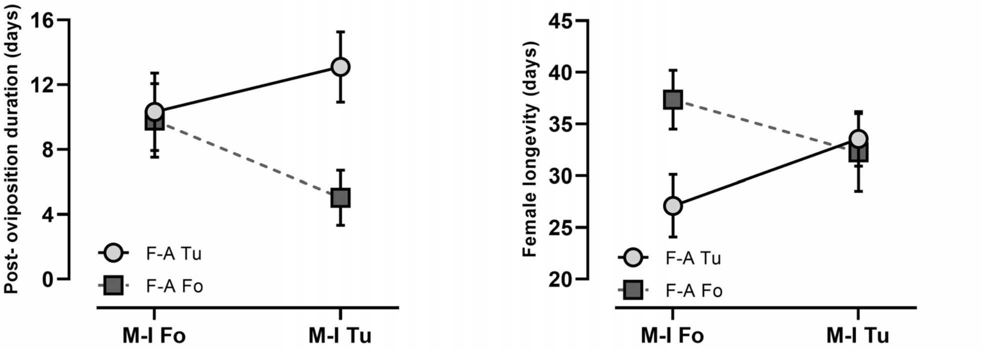

FIGURE 1. Mean (±SEM) post-oviposition duration and female longevity of *Neoseiulus californicus* as affected by prey of female adults (F-A) and male immatures (M-I).

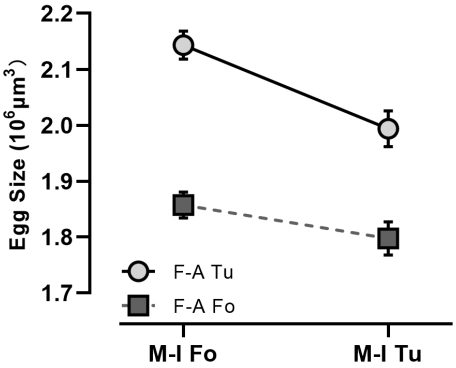

FIGURE 2. Mean (±SEM) egg size of *Neoseiulus californicus* as affected by prey of female adults (F-A) and male immatures (M-I).

TABLE 3. *Neoseiulus californicus* reproduction and offspring development in different feeding experience.

Treatments	Prey			Cumulative fecundity	Daily fecundity	Pre-oviposition (day)	Oviposition (day)	Post-oviposition (day)	Adult longevity (day)	Hatch rate	Proportion of female offspring	Egg volume ($10^6 \mu m^3$)	Developmental duration （day）
	F-A	F-I	M-I										
I	Tu	Tu	Tu	57.5±3.3	2.5±0.1	0.6±0.0	22.7±0.8	12.8±2.0	36.1±1.8	0.90±0.02	0.70±0.01	2.09±0.04	5.9±0.4
II	Tu	Tu	Fo	44.0±4.4	2.6±0.1	0.5±0.1	17.4±1.4	10.8±2.6	28.7±3.0	0.80±0.07	0.71±0.02	2.11±0.04	6.2±0.2
III	Tu	Fo	Tu	48.5±2.7	2.5±0.1	0.5±0.1	19.6±1.1	14.7±2.2	34.8±2.5	0.77±0.05	0.70±0.02	1.93±0.05	6.1±0.2
IV	Tu	Fo	Fo	43.5±3.2	2.6±0.1	1.0±0.2	16.8±1.3	10.75±2.3	28.6±2.7	0.85±0.02	0.70±0.01	2.14±0.05	5.4±0.1
V	Fo	Tu	Tu	39.9±5.2	1.7±0.1	0.9±0.1	23.4±3.0	8.0±1.7	32.3±4.2	0.82±0.04	0.69±0.01	1.80±0.05	6.1±0.2
VI	Fo	Tu	Fo	42.8±4.2	1.6±0.1	1.5±0.2	27.0±2.1	12.6±2.2	41.1±1.7	0.87±0.02	0.70±0.03	1.83±0.04	5.8±0.1
VII	Fo	Fo	Tu	45.0±3.8	1.7±0.1	1.7±0.2	28.2±3.2	2.65±1.2	32.6±3.6	0.87±0.02	0.69±0.02	1.80±0.03	5.3±0.2
VIII	Fo	Fo	Fo	34.2±2.7	1.6±0.1	2.7±0.4	22.7±2.2	7.5±2.1	32.8±3.5	0.82±0.04	0.67±0.02	1.84±0.05	5.6±0.1

F-A**,** prey species of female adults; F-I, prey species of female immatures; M-I, prey species of male immatures.

Impact of prey species on N. californicus *progeny development and sex allocation*

Eggs that developed to females were ca. 7.5% larger than those developed to males. In addition, egg size was significantly affected by prey species of female adults, male immatures, and the interaction between sex and prey of female immatures (Table 4). When female adults preyed on *T.*

urticae, their eggs were ca. 12.6% larger than those preyed on *F. occidentalis* (Figure 2, Table 3). In addition, eggs laid by females that mated with males preyed on *F. occidentalis* were ca. 5.5% larger than eggs with fathers preyed on *T. urticae* (Figure 2, Table 3). No significant impact of prey species on offspring developmental duration was observed. However, larger eggs tended to develop faster than small ones (Figure 3).

TABLE 4. Impact of parent prey and sex on egg size and developmental duration of *Neoseiulus californicus*.

Source	df	P	
		Egg volume	Developmental duration
F-I	1	0.251	0.788
M-I	1	**0.038**	0.822
F-A	1	**<0.001**	0.696
Sex	2	**<0.001**	0.802
F-I * Sex	1	**0.049**	0.547
M-I* Sex	1	0.401	0.501
F-A*Sex	1	0.430	0.815
M-I * F-I	1	0.148	0.073
F-I * F-A	1	0.318	0.616
M-I * F-A	1	0.602	0.815
Error	125		

F-A, prey species of female adults; F-I, prey species of female immatures; M-I, prey species of male immatures.

TABLE 5. The sex probability of the first egg of *Neoseiulus californicus* in different feeding experiences.

Treatments	Prey			Sex			
	F-A	F-I	M-I	Female		Male	
I	Tu	Tu	Tu	2	(22.2%)	7	(77.7%)
II	Tu	Tu	Fo	1	(14.3%)	6	(85.7%)
III	Tu	Fo	Tu	0	(0)	11	(100.0%)
IV	Tu	Fo	Fo	1	(9.1%)	10	(90.9%)
V	Fo	Tu	Tu	2	(20.0%)	8	(80.0%)
VI	Fo	Tu	Fo	2	(22.2%)	7	(77.7%)
VII	Fo	Fo	Tu	0	(0)	10	(100%)
VIII	Fo	Fo	Fo	2	(25%)	6	(75%)

F-A, prey species of female adults; F-I, prey species of female immatures; M-I, prey species of male immatures. Tu, *Tetranychus urticae*; Fo, *Frankliniella occidentalis*.

There was no significant difference in proportion of female offspring detected treatments, with an overall mean of 68.2%. Eighty-eight percentage of the first-laid eggs and at least one of first two eggs developed to males. The proportions of males among the first-laid eggs do not differ significantly across the treatments (χ^2=5.965, P =0.544) (Table 5). Four sex sequence patterns were observed for the first three eggs: MFF, MFM, MFF and FMF (M: male, F: female). The overall sex sequences do not differ significantly across the treatments (χ^2=23.543, P =0.316) (Table 6). Among the four sex sequence patterns, MFF was mostly observed (45%), followed by MFM (34%), FMF (12%), and the MMF (9%).

TABLE 6. The sex sequence of the first three egg of *Neoseiulus californicus* in different feeding experiences.

Treatments	Prey			Sex sequence of first three eggs							
	F-A	F-I	M-I	FMF		MFF		MFM		MMF	
I	Tu	Tu	Tu	2	(22.2%)	2	(22.2%)	5	(55.6%)	0	(0)
II	Tu	Tu	Fo	0	(0)	2	(66.7%)	1	(33.3%)	0	(0)
III	Tu	Fo	Tu	0	(0)	3	(42.85%)	1	(14.3%)	3	(42.85%)
IV	Tu	Fo	Fo	1	(11.1%)	4	(44.45%)	4	(44.45%)	0	(0)
V	Fo	Tu	Tu	1	(14.3%)	5	(71.4%)	1	(14.3%)	0	(0)
VI	Fo	Tu	Fo	1	(20.0%)	2	(40.0%)	2	(40.0%)	0	(0)
VII	Fo	Fo	Tu	0	(0)	5	(62.5%)	2	(25.0%)	1	(12.5%)
VIII	Fo	Fo	Fo	2	(25.0%)	2	(25.0%)	3	(37.5%)	1	(12.5%)

F-A, prey species of female adults; F-I, prey species of female immatures; M-I, prey species of male immatures. Tu, *Tetranychus urticae*; Fo, *Frankliniella occidentalis*.

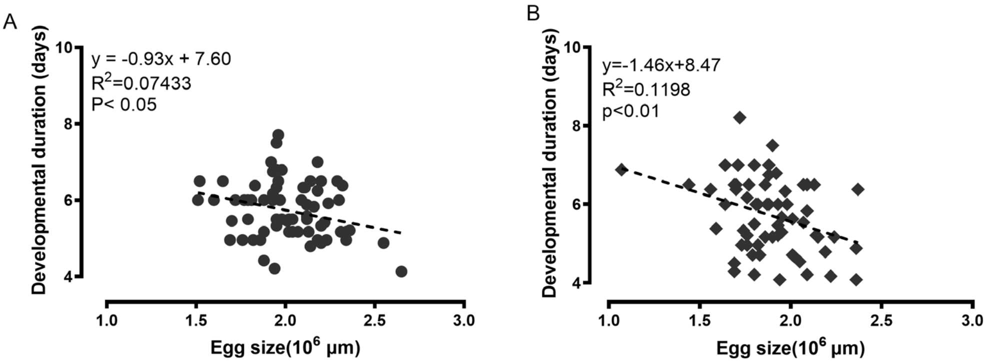

FIGURE 3. Correlation between *Neoseiulus californicus* egg size and developmental duration A, eggs develop to females. B, eggs develop to females.

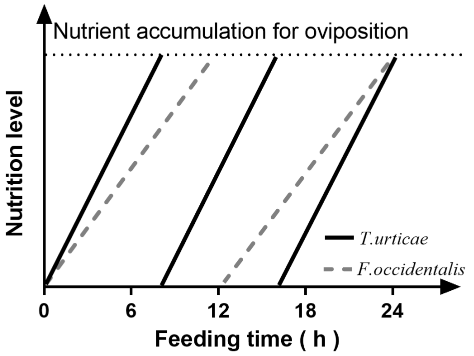

FIGURE 4. Assumed accumulated nutrition pattern for oviposition in *Neoseiulus californicus.*

Discussion

In this experiment, we found that females preyed on *F. occidentalis* or *T. urticae* have similar cumulative fecundity, but differed in daily fecundity. The average daily fecundity of females fed on *F. occidentalis* was 1.5 eggs/female/day, while that of those fed on *T. urticae* was 2.5 eggs/female/day (Table 3). In other words, *N. californicus* fed on *T. urticae* had shorter oviposition duration than those fed on *F. occidentalis* (Table 3). Based on these results, we assume that there might be a nutritional threshold for each egg formation (Jaumann & Snell-Rood 2019). Females might still be able to lay eggs when fed on prey of poor nutritional quality, but required longer time to accumulate nutrient. When *N. californicus* preyed on *F. occidentalis,* the process of egg maturation in was slower when preyed on *T. urticae* (Figure 4).

Poor nutrient of prey fed by *N. californicus* males or females in immature stages have negative impact on female reproduction, leading to the reduced fecundity and postponed oviposition duration. However, these negative impacts are relatively minor and reversible. If mated female had sufficient food of good quality, such negative impact was limited. These results are similar to some previous studies. Greco *et al.* (2006) reported that if *N. californicus* females starve for 2–4 days, their daily fecundity will be recovered in 2–3 days when sufficient preys are provided. Ogawa & Osakabe (2008) also reported that *N. californicus* females could recover fecundity when their food is switched from artificial diet to natural prey, *T. urticae*.

In this study, no significant impact of the prey species on offspring sex ratio was observed. In contrast, Abdel-Khalek & Momen (2009) reported that the proportion of *N. californicus* female offspring is 18.2% lower when fed on *T. evansi* than fed on *T. urticae*, but the lower proportion of female offspring is accompanied by 90% decrease in fecundity. Similarly, Toyoshima & Amano (1998) found that starvation may led to 90% decrease of fecundity and 50% decrease of proportion of female offspring in two phytoseiid mites, *P. persimilis* and *Amblyseius womersleyi* Schicha. In most phytoseiid species, eggs are dimorphism, with those develop to females are larger than those develop to males. It is assumed that female embryos have higher nutritional requirement, so they may suffer more from environmental pressure of limited or low quality of prey. When the mother is under poor nutritional conditions, more female embryos deceased during early development, especially before eggs were laid, which led to decreased proportion of female offspring. In contrast, limited changes in proportion of female offspring were expected when no significant decrease in cumulative fecundity was observed.

For selective and generalist phytoseiid species, field releases are usually performed when pest density is low or before pests reach the economic injury level, so-called Predator-In-First (Kutuk & Yigit 2011; Kumar *et al.* 2015). Thus the pest population are expected to be controlled as early as possible, with fewer predators released and lower economic costs. Therefore, predatory mites are expected to experience low prey density or hard hunting conditions after released. Both *T. urticae* and *F. occidentalis* are important greenhouse pests worldwide, while *F. occidentalis* has lower temperature threshold and optimal temperature for development (Hart *et al.* 2002; Kasap 2004; Chaisuekul & Riley 2005). Thus, *F. occidentalis* population often occur earlier in greenhouses than *T. urticae*. If *N. californicus* are released early in the season when there is only *F. occidentalis* in field, the fecundity would be 0.6–1.6 eggs per female per day (Van Baal *et al.* 2007), its population could still catch up the increase of *T. urticae* population when their fecundity compensated when better prey species available.

Momen (1994) showed that 17% *Neoseiulus barkeri* (Hughes) females mate with starved males fail to oviposit, others have shorter mating duration and lower daily fecundity compared to those mated with normal males. In the present study, female had longer pre-oviposition duration when they mated with males developed under poor nutritional conditions. In some insects, males transfer some nutritional contents (nuptial gift) to females during mating (Vahed 1998). For example, Immonena *et al.* (2009) reported that female *Drosophila subobscura* Collin under poor nutritional conditions prefer to mate with males grow under good nutritional conditions, so that they could increase their fecundity. Similar situations have also been observed in a few Acari species. van den Beuken & Smallegange (2018) reported that starved female bulb mite *Rhizoglyphus robini* Claparède mate with satiated males lay more eggs, and had higher proportions of female offspring. Phytoseiid males deliver spermatophores to females during mating. Investigating the contents in spermatophores, such as seminal fluid proteins as well as sperm, may provide evidences about functions of nuptial gifts in phytoseiids.

In this study, we investigated how feeding experiences of both males and females affect the reproduction of phytoseiid mites. Although females play dominant roles in reproduction regulation, nutritional stress of males may also affect their partners reproduction. Further studies are expected to investigate the mechanisms how males impact female reproduction, and to evaluate field release strategies under complicated prey species and density conditions.

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