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Article

Prey consumption and functional response of *Neoseiulus* californicus and *Neoseiulus longispinosus* (Acari: Phytoseiidae) on *Tetranychus urticae* and *Tetranychus kanzawai* (Acari: Tetranychidae)

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Abstract

Tetranychus urticae Koch and *Tetranychus kanzawai* Kishida are important pest mites of various crops of economic importance around the world. Prey consumption and functional responses of two species of phytoseiid mites on these two spider mites were evaluated at $25 \pm 1^{\circ}$ C, $65 \pm 10\%$ RH in the artificial climatic chamber with a photoperiod of 16 h light:8 h dark. The functional response of both *Neoseiulus* species was type II on three immature stages (egg, larva and protonymph) of *Tetranychus* species. The value of attack rate coefficients (α) of *N. californicus* to each stage of *Tetranychus* was greater than *N. longispinosus*, and the shortest handling time (T_h) was obtained on larvae followed by nymphs and eggs. The maximum attack rate (T/T_h) on eggs, larvae and nymphs of *T. urticae* was estimated to be 11.87, 37.23 and 26.95 for *N. californicus*, and 18.43, 28.98 and 20.67 for *N. longispinosus*; the maximum attack rate (T/T_h) on eggs, larvae and nymphs of *T. kanzawai* was estimated to be 11.90, 42.97 and 39.60 for *N. californicus*, and 24.15, 31.60 and 24.45 for *N. longispinosus*. When different densities of prey were offered to the predators, more prey was consumed at higher prey densities, and interaction between prey stage and prey density was significant for *N. californicus*, but not significant for *N. longispinosus*. The ability of *N. californicus* preying on larvae and nymphs of both *Tetranychus* species was significantly greater than *N. longispinosus* at high prey densities, but *N. longispinosus* consumed more eggs than *N. californicus*.

Key words: predatory capacity, two-spotted spider mite, red-mite, phytoseiid mites

Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch, is one of the most economically important pests on a wide range of crops around the world (Farazmand *et al.* 2012). Two forms are recognized in the two-spotted spider mite; one is the green form, which has green summer females, and other is the red form, which has reddish brown females (Goka *et al.* 1996). Both forms are distributed widely in China; the green form was named *T. urticae*, and the red form was named *T. cinnabarinus* (Boisduval) (Xie *et al.* 2006; Sun *et al.* 2012). The Kanzawai spider-mite, *T. kanzawai* Kishida is also red in color and similar to the red form of *T. urticae* in morphology and biology (Oku 2008; de Mendonca *et al.* 2011; Chen *et al.* 2014).

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Neoseiulus californicus (McGregor) is one of the most efficient biological control agents of tetranychid mites. It is widely distributed and has been commercially used in various countries around the world (Gotoh *et al.* 2004; Canlas *et al.* 2006; McMurtry *et al.* 2013; Barbosa & de Moraes 2015). *Neoseiulus longispinosus* (Evans) is another efficient phytoseiid mite of large number of mite pests, and this species has primarily an Asian distribution (Zhang *et al.* 1998; Thongtab *et al.* 2001; Carrillo *et al.* 2012; Rahman *et al.* 2013).

During several surveys of pest mites in Guangzhou, Guangdong Province, China, two *Tetranychus* species (*T. kanzawai* and *T. urticae*) and two *Neoseiulus* species (*N. californicus* and *N. longispinosus*) were found in the papaya field, in which the control of mite pests is usually carried out by spraying abamectin. In the first survey, only *T. kanzawai* and two phytoseiid mites were found. After two surveys, *T. kanzawai* disappeared, and only *T. urticae* was left (Song *et al.* 2013; 2014). In the first taxonomy of *Neoseiulus*, the *Neoseiulus* sp. was identified as *N. fallacis*, but in the following research Xu *et al.* (2013) classified this species to *N. californicus*; however there were some differences between Chinese specimens of *N. californicus* and the specimens collected from elsewhere (Xu *et al.* 2013; Lv *et al.* 2016).

Functional response is defined as the relationship between predation rates of a single predator at different densities of a prey per unit time (Farazmand *et al.* 2012). The functional response of phytoseiids is affected by a number of factors, such as different feeding history (Castagnoli & Simoni 1999), environmental temperature (Gotoh *et al.* 2004), different prey species (Escudero & Ferragut 2005) and the physical characteristics of host plant (Ahn *et al.* 2010). Functional response can show the efficiencies of studies and predation rates for predators and evaluate the ability of predators to regulate prey population (Xiao & Fadamiro 2010; Fathipour & Maleknia 2016).

In this study, we separately compared the functional response of *N. californicus* (Guangdong group) and *N. longispinosus* (an indigenous species) to two different *Tetranychus* species in the same conditions. The aim of this study was to see if the efficacies of *Neoseiulus* to the similar types of preys are different. The predation capacities of *N. californicus* and *N. longispinosus* to the *Tetranychus* are also compared in this study.

Material and methods

Prey Culture

Both species of *Tetranychus* (green form *T. urticae* and *T. kanzawai*) were originally collected from a papaya orchard in Nansha ($22^{\circ}42'N$, $113^{\circ}32'$), Guangzhou, China in 2011, and reared on bean (*Phaseolus vulgaris* L.) leaf discs (rearing arena) at $25 \pm 1^{\circ}C$, $65 \pm 10\%$ RH in an artificial climatic chamber with a photoperiod of 16 h light:8 h dark. The leaf discs were placed upside down on a water-saturated sponge, and the leaf edge was surrounded with strips of absorbent paper, in order to minimize the escape of individual mites and providing moisture. Every rearing unit was in a square plastic box ($15cm \times 15cm \times 6.5cm$) with a lid, which was holed and covered with fine nylon mesh to allow ventilation. The plastic boxes were filled with water until the water reached just below the leaf disc, and water was added every day.

Predator Source and Rearing

The colony of *N. californicus* and *N. longispinosus* were also collected together with *Tetranychus* in the same location. The predators were reared on the bean leaf disc filled with enough leaf mites (two *Tetranychus* species mixed). To obtain females predators of the same age for experiments, predator eggs were collected daily and transferred to a new arena with adequate leaf mites (two *Tetranychus* species mixed).

General Experimental Conditions

The experimental unit consisted in a bean leaf disc (3.5cm diameter) placed upside down on a water-saturated sponge (3.5cm diameter). The leaf discs were surrounded with strips of absorbent paper in order to minimize the escape of individual mites and provide moisture. Individuals trapped in the wet paper surrounding the leaf discs were excluded from data analysis. Every four test units were treated as one test group, and each test group was in a square plastic box as the rearing box. The plastic boxes were filled with water until the water level was just below the leaf disc, and water was added every day. All experiments were conducted at $25 \pm 1^{\circ}$ C, $65 \pm 10^{\circ}$ RH and a photoperiod of 16 h light:8 h dark. Before each test, the female adults (emerged in 48h) were fertilized and starved for 24h.

Each mite was transferred with fine hair brush to experimental unit for both functional response experiments, and individuals injured during the transfer were excluded from the experiments.

Functional Response

Seven densities of eggs, larvae and nymphs (protonymph) (2, 4, 8, 16, 32, 64 and 128 eggs, larvae or nymphs) of *T. urticae* and *T. kanzawai* were offered separately to the adult female of *N. californicus* and *N. longispinosus*. Each treatment was utilized 16 replicates. After 24h, the number of prey eaten was determined by counting intact eggs and the carcasses of larvae or nymphs.

The different densities of prey eggs were obtained as follows: 1-25 adult females of *Tetranychus* from the stock culture were introduced onto bean leaf disc (experimental unit) and allowed to lay eggs for 10-24 h at the experimental conditions, and then the females were removed. The numbers of prey eggs were adjusted for each experiment by removing excess eggs with a fine brush.

For prey larvae and nymphs, enough adult females of *Tetranychus* from the stock culture were introduced onto bean leaf disc, and allowed to lay eggs for 10 h at the experimental conditions, and then the females were removed. The discs with eggs were put in an artificial climatic chamber for their development. As soon as the larvae or nymphs emerged; the number of prey (larvae and nymphs) was transferred to the experimental unit with a fine brush.

Data Analysis

The data on functional response were analyzed in two steps (Juliano 2001). First, the logistic regression of the proportion of prey consumed (N_e/N_0) as a function of initial density (N_0) was used to determine the shape of the functional response. The data were fitted to a polynomial function that describes the relationship between the proportion of preys consumed and initial density:

 $N_{e}/N_{0} = \exp(P_{0} + P_{1}N_{0} + P_{2}N_{0}^{2} + P_{3}N_{0}^{3})/[1 + \exp(P_{0} + P_{1}N_{0} + P_{2}N_{0}^{2} + P_{3}N_{0}^{3})]$ (1)

where (N_e/N_0) is the probability a prey will be consumed, and P_0 , P_1 , P_2 and P_3 are the maximum likelihood estimates as being intercept, linear, quadratic and cubic coefficients respectively (Xiao & Fadamiro 2010). The values of P_0 , P_1 , P_2 and P_3 were estimated by using a cubic mathematical function for curve estimation (Table 1). The type of functional response was determined by fitting data to the model (1). The sign of P_1 and P_2 were used to distinguish the shape of the curves. When the function is negative ($P_1 < 0$), the predator displays a Type II functional response that indicates the proportion of prey consumed declines monotonically with the initial number of prey. When a positive density-dependent result for the proportion of prey consumed ($P_1 > 0$ and $P_2 < 0$) is obtained, the predator displays a Type III functional response (Juliano 2001)

Second, the handling time and the attack rate coefficients of a type II response were estimated using the random predator equation:

 $N_{\rm e} = N_0 \{1 - \exp[\alpha (T_{\rm h} N_{\rm e} - T)]\}$ (2)

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where N_e is the number of prey killed; N_0 is the initial number of prey; T_h is the handling time; and T is the total time available for predator. The data was analyzed using SAS software (SAS 2007). NLIN procedure in SAS was used to estimate the attack rate and the handling time parameters.

The effect of prey density on the daily consumption of *Neoseiulus* spp. was analyzed by oneway ANOVA followed by Tukey's test (P<0.05) (SAS 2007).

Results

The percentage of prey consumed for each prey stage declined with increasing prey density (Figure 1), which means inverse density-dependence, and the logistic regression for all prey stages had a significant linear parameter $P_1 < 0$ and positive quadratic coefficient (P_2) of the proportion of preys consumed at each density versus each initial density of prey (Table 1). This suggests that the functional response of both *Neoseiulus* species was type II on both stages of *Tetranychus* species. Therefore, the "random-predator" equation (2) for Type II was used to estimate the attack rate coefficient (α) and the handling time (T_h) (Table 2).

The value of attack rate coefficients (α) of *N. californicus* to each stage of *Tetranychus* was greater than that of *N. longispinosus*. The shortest handling time (T_h) of each *Neoseiulus* species was obtained when feeding on larvae of *Tetranychus*, followed by nymphs, the handling time (T_h) when feeding the eggs was the longest. The maximum attack rate (T/T_h) on eggs, larvae and nymphs of *T. urticae* was estimated to be 11.87, 37.23 and 26.95 for *N. californicus*, and 18.43, 28.98 and 20.67 for *N. longispinosus*; the maximum attack rate (T/T_h) on eggs, larvae and nymphs of *T. kanzawai* was estimated to be 11.90, 42.97 and 39.60 for *N. californicus*, and 24.15, 31.60 and 24.45 for *N. longispinosus* (Table 2). In other words, when *Neoseiulus* spp. was with three stages of prey (eggs, larvae and nymphs), they tended to consume more larvae, followed by nymphs and eggs.

For *N. californicus*, when different densities of prey were offered to the predators, more prey was consumed at higher densities of prey and the interaction between prey stage and different density was significant (Table 3). In other words, with increasing density of prey, most larvae were consumed in comparison to nymphs and eggs. For *N. longispinosus*, when different densities of prey were offered to the predators, the interaction between prey stage and different density was not significant (Table 3); with increasing density of prey, three stages of *Tetranychus* were consumed equally. The data of prey consumption also showed that *N. californicus* attacked more larvae and nymphs per day compared to *N. longispinosus*, and *N. longispinosus* attacked more eggs per day than *N. californicus*.

Discussion

Consumption rate of the predators is generally inversely related to prey size (Kasap & Atlihan 2011) but in this study, consumption rate of *N. californicus* of *Tetranychus* larvae was the highest, followed by the nymphs, and the consumption rate of eggs is the lowest. This might be due to the fact that larvae and nymphs of *Tetranychus* fed in clusters which make them relatively easy to handle them. Li *et al.* (2014) also tested the consumption rate of Chinese *N. californicus* feeding on *T. cinnabarinus* at 25°C, and the results showed that the ability of *N. californicus* controlling three stages of *T. cinnabarinus* was also larvae>nymphs>eggs. For *N. longispinosus*, although the mean consumption of *N. longispinosus* at different densities of three stages of *Tetranychus* spp. was not significantly different, the data showed that *N. longispinosus* consumed more eggs than larvae and nymphs; *N. longispinosus* preferred eggs more. Blackwood *et al.* (2001) tested *N. longispinosus* for

prey preferences between eggs and larvae, and the results showed that *N. longispinosus* had strong preference for eggs.

| Prey | | | Neoseiulus californicus | | | Neoseiulus longispinosi | ts | |
|----------------------|-------|------------|---|----------|----------|--|----------|----------|
| species | Stage | Parameters | Estimate (±SE) | χ^2 | Р | Estimate (±SE) | χ^2 | Р |
| | Egg | P_0 | 2.8425±0.2662 | 114.00 | < 0.0001 | 1.7882±0.2230 | 64.33 | < 0.0001 |
| | | P_1 | -0.1555 ± 0.0191 | 66.10 | < 0.0001 | -0.0786 ± 0.0165 | 22.74 | < 0.0001 |
| | | P_2 | $0.00174{\pm}0.000357$ | 23.82 | < 0.0001 | 0.000635 ± 0.000311 | 4.18 | 0.0410 |
| | | P_3 | $-6.51{\times}10^{\text{-}6}{\pm}1.758{\times}10^{\text{-}6}$ | 13.73 | 0.0002 | $-1.877{\times}10^{\text{-6}}{\pm}1.537{\times}10^{\text{-6}}$ | 1.48 | 0.2235 |
| | Larva | P_0 | 3.3110±0.3801 | 75.87 | < 0.0001 | 0.3852 ± 0.1883 | 4.18 | 0.0408 |
| | | P_1 | -0.0730 ± 0.0254 | 8.26 | 0.0040 | -0.0556 ± 0.0151 | 13.52 | 0.0002 |
| | | P_2 | 0.000475 ± 0.00451 | 1.11 | 0.2923 | 0.000674 ± 0.000294 | 5.25 | 0.0220 |
| ae. | | P_3 | $-1.331 \times 10^{-6} \pm 2.156 \times 10^{-6}$ | 0.38 | 0.5366 | $-2.83{\times}10^{\text{-}6}{\pm}1.471{\times}10^{\text{-}6}$ | 3.70 | 0.0545 |
| urtic | | P_0 | 2.0207±0.2435 | 68.87 | < 0.0001 | -0.1889 ± 0.1917 | 0.97 | 0.3245 |
| chus | | P_1 | -0.0593 ± 0.0175 | 11.53 | 0.0007 | -0.0326 ± 0.0156 | 4.39 | 0.0361 |
| Tetranychus urticae | Nymph | P_2 | 0.000193±0.000324 | 0.35 | 0.5514 | 0.000250 ± 0.000305 | 0.67 | 0.4127 |
| Tetr | | P_3 | $5.035{\times}10^{7}{\pm}1.589{\times}10^{6}$ | 0.10 | 0.7514 | $-8.03{\times}10^{\text{-7}}{\pm}1.531{\times}10^{\text{-6}}$ | 0.27 | 0.6000 |
| | _ | P_0 | 2.8425 ± 0.2662 | 114.00 | < 0.0001 | 2.1361±0.2395 | 79.53 | < 0.0001 |
| | | P_1 | -0.1555 ± 0.0191 | 66.10 | < 0.0001 | -0.0913 ± 0.0173 | 27.81 | < 0.0001 |
| | Egg | P_2 | 0.00174 ± 0.000357 | 23.82 | < 0.0001 | 0.000786±0.000323 | | 0.0149 |
| | | P_3 | $-6.51{\times}10^{\text{-}6}{\pm}1.758{\times}10^{\text{-}6}$ | 13.73 | 0.0002 | $-2.28{\times}10^{\text{-}6}{\pm}1.586{\times}10^{\text{-}6}$ | 2.07 | 0.01503 |
| i | Larva | P_0 | 3.7338 ± 0.3885 | 92.39 | < 0.0001 | 0.6134 ± 0.1893 | 10.50 | 0.0012 |
| | | P_1 | -0.1254 ± 0.0253 | 24.66 | < 0.0001 | -0.0522 ± 0.0150 | 12.14 | 0.0005 |
| | | P_2 | 0.00142 ± 0.000442 | 10.28 | 0.0013 | 0.000532±0.000290 | 3.37 | 0.0665 |
| awa | | P_3 | $-5.62{\times}10^{\text{-}6}{\pm}2.103{\times}10^{\text{-}6}$ | 7.14 | 0.0076 | $-1.97{\times}10^{\text{-}6}{\pm}1.447{\times}10^{\text{-}6}$ | 1.86 | 0.1727 |
| kanz | Nymph | P_0 | 3.2211±0.2987 | 116.29 | < 0.0001 | 0.6896 ± 0.1908 | 13.06 | 0.0003 |
| Tetranychus kanzawai | | P_1 | -0.1545 ± 0.0203 | 57.78 | < 0.0001 | -0.0750 ± 0.0153 | 23.91 | < 0.0001 |
| ranyı | | P_2 | 0.00201 ± 0.000365 | 30.19 | < 0.0001 | $0.000965{\pm}0.000298$ | 10.47 | 0.0012 |
| Teth | | P_3 | $-8.3{\times}10^{\text{-}6}{\pm}1.763{\times}10^{\text{-}6}$ | 22.16 | < 0.0001 | $-4.13{\times}10^{\text{-6}}{\pm}1.493{\times}10^{\text{-6}}$ | 7.64 | 0.0057 |

TABLE 1. Maximum likelihood estimates from logistic regression of proportion of prey consumed as a function of initial prey densities by adults of *Neoseiulus californicus* and *N. longispinosus*.

The data from the logistic regression indicate that both *N. californicus* and *N. longispinosus* exhibited typical type II functional response on three immature stages of *Tetranychus* spp. Similar data were obtained for Chinese *N. californicus* (Qin & Li 2013; Li *et al.* 2014; Wang *et al.* 2014) and *N. longispinosus* (Zhang *et al.* 1998). Predators with higher searching efficiency (α) and lower handling time (T_h) are better agents, although predators exhibiting the Type III functional response are efficient biocontrol agents. Many of the predators that have been successfully released as biological control agents have shown the Type II functional response on their prey (Fathipour & Maleknia 2016).

In previous reports, *N. longispinosus* was considered to be oligophagous, specialized spider mite predators; and *N. californicus* was considered to be more polyphagous, generalist predators (Blackwood *et al.* 2001). However, Croft *et al.* (2004) suggested *N. californicus* should be the same type as *N. longispinosus*. In this manuscript, we showed that *N. californicus* was more effective

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against *Tetranychus*'s larvae and nymphs than *N. longispinosus*, and *N. longispinosus* was more effective against *Tetranychus*'s eggs.

| | | Neoseiulus californio | cus | | |
|--------------|-------|-----------------------|----------------------|---------------|-------|
| Prey species | Stage | $a (h^{-1})$ | $T_{\rm h}({\rm h})$ | $T/T_{\rm h}$ | r^2 |
| | | 0.1721 ± 0.0408 | 2.0213±0.0679 | 11.87 | 0.948 |
| | Egg | (0.0912-0.2530) | (1.8867–2.1559) | | |
| Tetranychus | | 0.2503 ± 0.0704 | 0.6446±0.0275 | 37.23 | 0.951 |
| urticae | Larva | (0.1108–0.3897) | (0.5900-0.6992) | | |
| | | 0.0960±0.0149 | 0.8905±0.0387 | 26.95 | 0.948 |
| | Nymph | (0.0665–0.1255) | (0.8137–0.9673) | | |
| | | 0.3285±0.1322 | 2.0174±0.0671 | 11.90 | 0.948 |
| | Egg | (0.0665–0.5906) | (1.8844–2.1504) | | |
| Tetranychus | | 0.1229±0.0190 | 0.5585 ± 0.0250 | 42.97 | 0.959 |
| kanzawai | Larva | (0.0853-0.1606) | (0.5089–0.6081) | | |
| | | 0.0562 ± 0.0082 | 0.6061±0.0437 | 39.60 | 0.925 |
| | Nymph | (0.0400-0.0725) | (0.5195–0.6926) | | |
| | | Neoseiulus longispin | osus | | |
| Prey species | Stage | $a (h^{-1})$ | $T_{\rm h}({\rm h})$ | $T/T_{\rm h}$ | r^2 |
| | | 0.1196±0.0307 | 1.3020±0.0698 | 18.43 | 0.900 |
| | Egg | (0.0588–0.1804) | (1.1637–1.4403) | | |
| Tetranychus | | 0.0257 ± 0.0039 | 0.8281 ± 0.0867 | 28.98 | 0.883 |
| urticae | Larva | (0.0180-0.0335) | (0.6563–0.9998) | | |
| | | 0.0225±0.0037 | 1.1611±0.1162 | 20.67 | 0.865 |
| | Nymph | (0.0152–0.0298) | (0.9307–1.3914) | | |
| | | 0.0772±0.0259 | 0.9937±0.1033 | 24.15 | 0.764 |
| | Egg | (0.0259–0.1285) | (0.7890–1.1983) | | |
| Tetranychus | | 0.0301±0.0038 | 0.7595±0.0625 | 31.60 | 0.922 |
| | Larva | (0.0226–0.0376) | (0.6356–0.8835) | | |
| kanzawai | | | | | |
| | | 0.0281±0.0037 | 0.9817±0.0766 | 24.45 | 0.912 |

TABLE 2. Estimate (±SE) of instantaneous attack rate and handling time of *Neoseiulus californicus* and *N. longispinosus* feeding on different stages of *Tetranychus urticae* and *T. kanzawai*

Notes: The values are presented as mean \pm SE. The values in parentheses represent 95% confidence intervals. *a*, attack rate; $T_{\rm h}$, handling time; $T/T_{\rm h}$, maximum attack rate.

Comparing the mean daily consumption of *Neoseiulus* spp. at different densities of different stages of *Tetranychus urticae* and *T. kanzawai*, more *T. kanzawai* larvae and nymphs were consumed by *Neoseiulus* spp, although the differences were not significant after analyzed by ANOVA followed by Tukey's test. In the draft of this paper, we analyzed the data by Duncan's Multiple Range Test, and the results showed that the mean daily consumption of *Neoseiulus* spp. at the higher densities of

T. urticae and *T. kanzawai* were significantly different. This showed that the Tukey's test was more appropriate and precise for multiple comparisons in this paper.

| Prey species | Prey | | Larva | | |
|-------------------------|--------------------------------------|--|---|---|--|
| riey species | density | N. californicus | N. longispinosus | N. californicus | |
| | 2 | 1.38±0.22 f AB | 1.69±0.15 e A | $1.56\pm0.18~\mathrm{eAB}$ | |
| | 4 | $3.06\pm0.31~\mathrm{f}~\mathrm{ABC}$ | 2.13 ± 0.34 e BCD | 3.63 ± 0.18 de A | |
| | 8 | 7.19±0.29 e A | 6.50 ± 0.42 de A | 7.81 ± 0.14 d A | |
| Tetranychus urticae | 16 | 9.69 ± 0.33 cd C | 12.69 ± 0.46 bcd B | 15.38±0.29 c A | |
| unicae | 32 | 9.75 ± 0.57 cd CD | 13.25 ± 1.09 bcd C | 24.94 ± 0.93 b A | |
| | 64 | 11.25 ± 0.42 abc C | $16.00 \pm 1.43 \text{ b BC}$ | 35.94 ± 1.65 a A | |
| | 128 | 12.19 ± 0.96 ab D | 18.31 ± 1.70 ab CD | 33.19±2.57 a A | |
| | 2 | $1.63 \pm 0.18 \text{ f A}$ | 1.69±0.15 e A | 1.63±0.15 e A | |
| | 4 | 3.50 ± 0.18 f AB | 2.19±0.32 e C | 3.63 ± 0.15 de A | |
| | 8 | 7.56 ± 0.16 de A | 7.19±0.33 cde A | $7.88 \pm 0.09 \text{ d A}$ | |
| Tetranychus kanzawai | 16 | 10.38±0.58 bc C | 13.13 ± 0.66 bcd AB | 15.00 ± 0.56 c A | |
| καπζανναι | 32 | 11.75±0.43 abc CD | 13.94 ± 0.85 bc BC | 22.56 ± 0.89 b A | |
| | 64 | 10.00 ± 0.37 bc D | 16.56±1.22 b C | 32.88 ± 1.56 a A | |
| | 128 | 12.81±1.05 a D | $24.19\pm\!4.62~\mathrm{a}~\mathrm{BC}$ | 37.88±2.38 a A | |
| D | Prey | Larva Ny | | mph | |
| Prey species | density | N. longispinosus | N. californicus | N. longispinosus | |
| | 2 | $0.88\pm0.18~\mathrm{i}~\mathrm{B}$ | $1.56\pm0.18\mathrm{hAB}$ | $1.00\pm0.18~\mathrm{h~AB}$ | |
| | 4 | 2.06 ± 0.23 hi CD | 3.25 ± 0.28 gh AB | 1.75 ± 0.28 gh D | |
| | 8 | 4.56 ± 0.48 ghi B | 7.00 ± 0.32 g A | 2.88 ± 0.40 fgh C | |
| Tetranychus | | | | | |
| - | 16 | 6.50 ± 0.49 fgh D | 12.25±0.89 ef B | 5.50±0.66 efg D | |
| urticae | 16 32 | 6.50±0.49 fgh D 9.81±0.90 ef CD | 12.25±0.89 ef B 18.38±1.05 cd B | 5.50±0.66 efg D 8.69±0.99 cde D | |
| - | | 0 | | e e | |
| - | 32 | 9.81±0.90 ef CD | $18.38 \pm 1.05 \text{ cd B}$ | 8.69 ± 0.99 cde D | |
| - | 32 64 | 9.81±0.90 ef CD 15.38±1.38 cd BC | 18.38±1.05 cd B 19.19±0.80 cd B | 8.69 ± 0.99 cde D 12.00 ± 1.00 bc C | |
| - | 32 64 128 | 9.81±0.90 ef CD 15.38±1.38 cd BC 21.00±2.00 ab BC | 18.38±1.05 cd B 19.19±0.80 cd B 26.25±1.49 b AB | 8.69±0.99 cde D 12.00±1.00 bc C 15.88±1.63 ab CD | |
| urticae | 32 64 128 2 | 9.81 \pm 0.90 ef CD 15.38 \pm 1.38 cd BC 21.00 \pm 2.00 ab BC 1.06 \pm 0.17 i A | 18.38±1.05 cd B 19.19±0.80 cd B 26.25±1.49 b AB 1.75±0.14 h A | 8.69 ± 0.99 cde D 12.00 ± 1.00 bc C 15.88 ± 1.63 ab CD 1.19 ± 0.21 h A | |
| urticae Tetranychus | 32 64 128 2 4 | 9.81 \pm 0.90 ef CD 15.38 \pm 1.38 cd BC 21.00 \pm 2.00 ab BC 1.06 \pm 0.17 i A 2.13 \pm 0.30 hi C | 18.38±1.05 cd B 19.19±0.80 cd B 26.25±1.49 b AB 1.75±0.14 h A 3.56±0.16 gh AB | 8.69 \pm 0.99 cde D 12.00 \pm 1.00 bc C 15.88 \pm 1.63 ab CD 1.19 \pm 0.21 h A 2.56 \pm 0.33 fgh BC | |
| urticae | 32 64 128 2 4 8 | 9.81 \pm 0.90 ef CD 15.38 \pm 1.38 cd BC 21.00 \pm 2.00 ab BC 1.06 \pm 0.17 i A 2.13 \pm 0.30 hi C 5.06 \pm 0.38 ghi B | 18.38±1.05 cd B 19.19±0.80 cd B 26.25±1.49 b AB 1.75±0.14 h A 3.56±0.16 gh AB 7.44±0.20 fg A | 8.69 \pm 0.99 cde D 12.00 \pm 1.00 bc C 15.88 \pm 1.63 ab CD 1.19 \pm 0.21 h A 2.56 \pm 0.33 fgh BC 4.38 \pm 0.42 fgh B | |
| urticae Tetranychus | 32 64 128 2 4 8 16 | 9.81 \pm 0.90 ef CD 15.38 \pm 1.38 cd BC 21.00 \pm 2.00 ab BC 1.06 \pm 0.17 i A 2.13 \pm 0.30 hi C 5.06 \pm 0.38 ghi B 7.69 \pm 0.45 efg D | $18.38 \pm 1.05 \text{ cd B}$ $19.19 \pm 0.80 \text{ cd B}$ $26.25 \pm 1.49 \text{ b AB}$ $1.75 \pm 0.14 \text{ h A}$ $3.56 \pm 0.16 \text{ gh AB}$ $7.44 \pm 0.20 \text{ fg A}$ $12.63 \pm 0.54 \text{ e B}$ | 8.69 \pm 0.99 cde D 12.00 \pm 1.00 bc C 15.88 \pm 1.63 ab CD 1.19 \pm 0.21 h A 2.56 \pm 0.33 fgh BC 4.38 \pm 0.42 fgh B 6.56 \pm 0.41 def D | |

TABLE 3. Mean (±SE) daily consumption of *Neoseiulus californicus* and *N. longispinosus* at different densities of different stages of *Tetranychus urticae* and *T. kanzawai*

Notes: The means followed by different small letters in the table are significantly different (p<0.05, Tukey's test) in the same column, the values followed by different capital letters in the table are significantly different (p<0.05, Tukey's test) in the same line. The values are presented as mean \pm SE

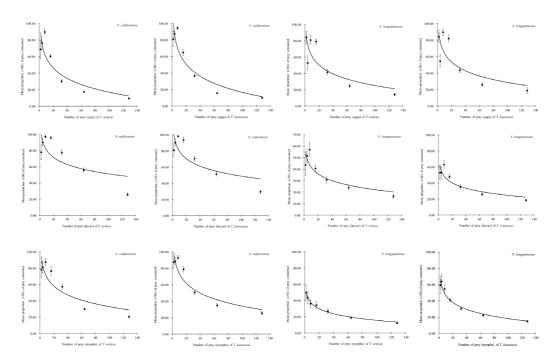


FIGURE 1. Mean proportion (±SE) of prey consumed by adult females of *Neoseiulus californicus* and *N. longispinosus* at seven densities of three stages of *Tetranychus urticae* and *T. kanzawai*.

Phytoseiids are able to perceive chemical cues produced by their spider-mite prey; these chemical compounds involved were called "kairomones" (Sabelis & Van de Baan 1983; Sabelis& Dicke 1985; Dicke & Sabelis 1988; Dicke et al. 1990). Recent research shows that these chemical volatiles were produced by plants infected by herbivores; the volatiles emitted from the plant are called "HIPVs" (herbivore-induced plant volatiles) (Takabayashi et al. 1994; Shimoda et al. 2005; Nachappa et al. 2006; Dicke & Baldwin 2010; Dicke 2015). "HIPVs" comprise a complex mixture of tens up to more than 200 compounds, the composition of which may vary with herbivore species, herbivore developmental instar, plant tissue, and abiotic conditions (Dicke 2015). In this study, at the high density of each prey stage, N. californicus consumed more Tetranychus's larvae and nymphs than eggs, because the volatiles are concentrated at the lower epidermis of the leaves, which are exploited by the spider mites. The more prey on the leaf, the more HIPVs are released (Sabelis & Van de Baan 1983); the larvae and nymphs of spider mites damaged the leaf more directly than the eggs; N. californicus would sense more volatiles from leaves infested with Tetranychus larvae and nymphs. However, N. longispinosus consumed three stages of Tetranychus spp. equally, and the predatory ability of N. longispinosus was lower than the predatory ability of N. californicus; perhaps the abilities of sensing HIPVs between these two Neoseiulus spp. were different. N. californicus and N. longispinosus are all good candidates for the control of Tetranychus mites. To confirm the relationship between the predatory abilities and chemosensory abilities, the chemical sense capacities of these two *Neoseiulus* spp. to differently treated bean leaves should be measured by the olfactometer, then by SEM and TEM to confirm the composition and structure of the olfactory system.

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