

THE EFFECT OF TEMPERATURE ON THE FUNCTIONAL RESPONSE AND PREY CONSUMPTION OF *PHYTOSEIUS PLUMIFER* (ACARI: PHYTOSEIIDAE) ON THE TWO-SPOTTED SPIDER MITE

M. Kouhjani Gorji, Y. Fathipour* and K. Kamali

Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P.O. Box: 14115-336, Tehran, Iran; e-mail: fathi@modares.ac.ir

ABSTRACT: The purpose of this study was to determine the relationship between prey density and consumption by the mated female of *Phytoseius plumifer* (functional response) and the voracity of different life stages. The *Phytoseius plumifer* females were fed on nymphal stages of *Tetranychus urticae* Koch at four different temperatures (15, 20, 25 and 30°C) and six prey densities ($n=2, 4, 8, 16, 32$ and 64) for 24 hours. The functional response and prey consumption experiments were carried out at six temperatures (15, 20, 25, 30, 35 and 37°C). The results showed that the functional response of *P. plumifer* to different densities of *Tetranychus urticae* at all temperatures was type II (the proportion of preys consumed declines monotonically with a prey density). The maximum searching efficiency was observed at 25°C ($a = 0.059 \text{ h}^{-1}$) and the minimum handling time was observed at 30°C and was calculated as $T_h = 0.425 \text{ h}$. The number of preys consumed daily and totally by the protonymphal stage increased with increasing temperature from 15°C (0.71 and 3.97, respectively) to 25°C (2.37 and 5.44, respectively) and then decreased until 35°C. The daily prey consumption of the deutonymphs ranged from 1.30 to 5.46 at 15 and 35°C, respectively. The daily prey consumption of the females increased with temperature from 8.85 preys/day at 15°C to 31.81 preys/day at 35°C. The total female prey consumption increased with temperature from 218.30 preys at 15°C to 426.98 preys at 25°C.

KEY WORDS: Functional response, *Phytoseius plumifer*, Predation, Temperature, *Tetranychus urticae*

INTRODUCTION

Temperature is the major abiotic factor that influences the biology of pests and their natural enemies. In the field of biological control, the details of responses to such factors are useful for the selection of natural enemies that are best adapted to the conditions that favor the target pest (Obrycki and Kring 1998).

The two-spotted spider mite, *Tetranychus urticae* Koch, is a serious pest of many plant species in both greenhouse and outdoor conditions (Cagle 1949). Because of its high numbers and reproductive rates, management of *T. urticae* can be difficult. Traditionally, *T. urticae* has been managed with acaricides, but these are not always effective. Their use may also result in problems of pesticide resistance and residues on the harvested and consumed products (Cranham and Helle 1985; Hussey and Scopes 1985; Brandenburg and Kennedy 1987; Campos and Omoto 2002).

Various natural enemies play an important role in the ecology of pest species, for example, predaceous mites in the family Phytoseiidae are important natural enemies of several phytophagous mites and other pests on various crops (McMurtry and Croft 1997). More specifically, some of them are used to control phytophagous mites in orchards (McMurtry et al. 1970; Tanigoshi et al. 1983). The predatory mite *Phytoseius plumifer* (Canestrini and Fanzago) has been reported from different countries (e.g., Zaher et al. 1969; Sepasgolian 1975; Castagnoli and Liguori 1985; Tix-

ier et al. 1998). Some biological parameters of *P. plumifer* have been studied by some researchers (Zaher et al. 1969; Rasmy and El-Banhawy 1974; El-Bagoury and Naser 1984; Gomaa and Reda 1985; Nawar et al. 2001) but no one tested the effect of different temperatures on a functional response and prey consumption of this predator. One of the fundamental aspects of a predator-prey interaction is the relationship between prey density and consumption by predators, to which Solomon (1949) attributed the term “functional response”, according to Holling (1959, 1961). Factors that affect parameters in functional response models include temperature, substrate and application of chemicals (Zhang et al. 1999).

There are four basic types of functional response: 1. A linear rise to a plateau (type I), 2. A curvilinear rise to a plateau (type II); type I and II responses are found in most invertebrates, 3. A sigmoid curve also reaching a plateau (type III) that is more usual in vertebrates, although some arthropods can also show this response when their preferred prey is not available (Hassell et al. 1977; Jervis and Kidd 1996). 4. A dome-shaped response (type IV), which has been reported on *Phytoseius persimilis* attacking *T. urticae* (Mori and Chant 1966).

Understanding of the influence of temperature on the interactions between pests and their associated natural enemies is crucial in determining future strategies for biological control. The objec-

tive of this study was to determine the effect of different temperatures on voracity (prey consumption) and the functional response of *P. plumifer* to varying densities of *T. urticae*. We discuss the optimal temperatures to use in a biological control against *T. urticae*.

MATERIALS AND METHODS

Mite cultures. The predator, *P. plumifer*, was originally collected from unsprayed fig orchards near Varamin, in the central part of Iran, during July 2006. Fig leaves containing the predator were cut and transferred to the laboratory. The predator mites were picked out using a fine soft pointed brush and released into a rearing arena. The laboratory cultures in each colony were initiated from 30 females and 30 males and total laboratory cultures were more than 1500 mites. The rearing arena was constructed from two plastic Petri dishes. The smaller dish (8 cm diameter × 1.5 cm height), with its base drilled centrally (1 cm diameter), was placed inside the larger one (9 cm diameter × 1.5 cm height) to supply water to the arena. The upside down life disc was placed on the smaller Petri dish. Layer of cotton 2 mm thick was placed in the smaller dish to keep the fig leaves fresh. Fig leaf discs (6 cm in diameter) were surrounded with water-saturated cotton tissue to prevent escape of the mites.

In order to keep the humidity in the arena constant, water was added to the cotton every day. The colonies were fed with an appropriate number of nymphal stages of *T. urticae* and corn pollen. Corn and date pollen accelerated the development of *Amblyseius gossipi* Elbadry but it reproduced at a similar rate on either a pollen or mite diet (Elbenhay 1968). Further experiments are necessary to determine the efficiency of the predator under field conditions (Zaher et al. 1969). Maize pollen was collected in the summer of same year with a fine soft pointed brush and preserved in a refrigerator at 4 °C. The predator mites were reared on fig leaves in a growth chamber at 27±1°C, with 50±10% relative humidity (RH) and a photoperiod of 16:8 h (L:D).

Two-spotted spider mite colonies were maintained on the common bean (*Phaseolus vulgaris* Linnaeus, variety Sayad). They were grown initially in a greenhouse at 32±1°C, with 50±10% RH and a photoperiod of 16:8 h L:D. The spider mite individuals used to initiate the colonies were collected from infested weeds at the Faculty of Agriculture of Tarbiat Modares University (Tehran) and then released on the bean plants.

Functional response study. The experimental arena was prepared using Petri dishes of 3.5 cm diameter × 1.2 cm height and 6 cm diameter × 1cm height as the same manner as rearing colony. The newly emerged *P. plumifer* females and males were placed in the experimental arena for a 24 hour period of starvation. After 24 hours, the males were removed from the arena and each female was fed with initial prey densities of 2, 4, 8, 16, 32, and 64 nymphal stages of *T. urticae* because of their lower silken web within stages. The prey mites were picked out using a fine soft pointed brush and released into experimental arenas. The arenas were placed in a growth chamber with a relative humidity of 50±10%, a photoperiod of 16:8 h L:D at four different temperatures, 15, 20, 25 and 30±1°C. Each treatment was tested with 14 replications. The number of prey killed per predator was recorded after 24 hours of exposure.

Data analysis of functional response. It is difficult to discriminate between functional responses of types II and III. Therefore, prior to fitting the data to Holling and Rogers' equations, cubic logistic regression analysis of the proportion of prey consumed (Na/N_i) and prey density (N_i) was performed to determine the shape of the functional response (e.g., type II or III) (Juliano 2001).

$$\frac{Na}{N_i} = \frac{\exp(P_0 + P_1N_i + P_2N_i^2 + P_3N_i^3)}{1 + \exp(P_0 + P_1N_i + P_2N_i^2 + P_3N_i^3)}$$

where Na is the number of prey consumed, N_i is the initial number of prey, the intercept P_0 and linear, quadratic, and cubic coefficients (P_1 , P_2 , and P_3), estimated using the maximum likelihood method (Juliano 2001). Significant negative or positive linear coefficients (i.e., P_1) from the regression analysis indicate type II or III responses, respectively (Juliano 2001). The handling times and attack coefficients of a type II response were estimated using both Holling's disc equation (Holling 1959) and Rogers' random attack equation (Rogers 1972) as follows:

$$N_a = \frac{aN_i}{1 + aT_h} \quad \text{Holling type II}$$

$$N_a = N_i[1 - \exp(-aTP_i/1 + aT_hN_i)] \quad \text{Rogers type II}$$

where N_a is the number of prey consumed, N_i the initial density of prey, T the time available for searching during the experiment, a the instantaneous attack rate, P_i the number of predators and T_h the amount of time the predator handles each prey individual (handling time). The functional re-

sponse models were estimated using SAS PROC NLIN (SAS Institute 1996).

Effect of temperature on prey consumption of *P. plumifer*. The experiment was conducted in the same manner as the functional response study. The experimental arenas were located in the laboratory under ambient conditions at six constant temperatures (15, 20, 25, 30, 35 and 37°C), with 50±10% RH and a photoperiod of 16:8 h L:D. After emergence of larvae, individuals were checked daily and the consumed nymphal stages of *T. urticae* were counted and replaced with live individuals until they reached the adult stage. Larvae of *P. plumifer* do not feed; therefore the purpose of this study was to determine the effect of temperature on the prey consumption of protonymphs and deutonymphs of the predator for the nymphal stages of the prey species *T. urticae*. Males and females were paired, and male consumption was ignored because it was low and negligible (average of 2–3 preys per day). Ten, twenty, thirty and forty individual of protonymphs and deutonymphs of the prey were supplied. The number of prey offered was in excess of consumption, based on preliminary experiment. Dead males were replaced with other individuals that lived in the same condition as the female. Each adult couple was held in a leaf disc and checked daily for prey consumption until the death of the last adult. The number of prey killed by adult couple was recorded daily. Corn pollen was added to the leaf arenas daily as additional food. Each treatment was tested with 50 and 15 replications for the immature and mature stages, respectively.

Analysis of prey consumption data. Live and dead mites found in the wet cotton barrier during the daily checks on each stage were excluded from the data analysis for that stage. Analysis of variance (ANOVA) was used to compare predator prey consumption at different temperatures using SPSS v. 13.0 (SPSS 2004). If signifi-

cant differences were detected, multiple comparisons were made using the LSD test with a significance level of 0.01.

RESULTS

Effect of temperature on functional response of *P. plumifer*. The logistic regression analysis of the functional response of *P. plumifer* at all temperatures had a negative slope for the linear coefficient (Table 1).

Rogers type II model was fitted separately for each temperature in order to compare the search rates and handling times at different temperatures. Holling and Rogers type II models fitted the data for *P. plumifer* at different temperatures. However, the estimated values of R^2 for the Holling type II model were slightly higher. But, we used the Rogers type II model to estimate the instantaneous attack rate (a) and handling time (T_h) because for this type of experiment without replacement of consumed prey in short time intervals, the Royama or Rogers model should be used (Hassell et al. 1977). The search rate or instantaneous attack rate defines how steeply the curve approaches the upper asymptote and is the estimated proportion of the area searched during the experimental interval (Gitonga et al. 2002).

The inverse of handling time, the handling rate, is the upper asymptote of the functional response curve, and represents the potential number of prey that could be predated during one experimental interval (Cave and Gaylor 1987). Using the Rogers type II model, the R^2 values for *P. plumifer* at different temperatures ranged from 0.945 to 0.941. The R^2 values and estimated parameters of the functional response at different temperatures are shown in Table 2.

Our results indicate that the maximum searching efficiency was at 25°C ($a = 0.059 \text{ h}^{-1}$) and the estimated minimum handling time ($T_h = 0.425 \text{ h}$) occurred at 30°C. The attack rate and handling time

Table 1
Estimated parameter of logistic regressions of the proportion of prey killed against the number of prey offered (N_p) for the female adults of *Phytoseius plumifer* at different temperatures

| Temperature (°C) | Parameter | | | |
|------------------|---------------------|------------------|---------------------|-----------------|
| | Intercept (P_0) | Linear (P_1) | Quadratic (P_2) | Cubic (P_3) |
| 15 | 1.48 | -0.24 | 0.008 | -0.00008 |
| 20 | 1.07 | -0.10 | 0.003 | -0.00002 |
| 25 | 1.92 | -0.10 | 0.002 | -0.00001 |
| 30 | 1.66 | -0.13 | 0.002 | -0.00001 |

Table 2
Estimated parameters of functional responses of *Phytoseius plumifer* females on nymphal stages of *Tetranychus urticae* at different temperatures

| Parameter | 15°C | 20°C | 25°C | 30°C |
|-----------|-------------------|-------------------|-------------------|-------------------|
| T/T_h | 48.8 | 47.4 | 36.8 | 56.5 |
| T_h | 0.492 (0.29–0.69) | 0.506 (0.38–0.63) | 0.651 (0.52–0.78) | 0.425 (0.23–0.62) |
| a | 0.027 (0.02–0.03) | 0.037 (0.03–0.04) | 0.059 (0.04–0.07) | 0.030 (0.02–0.04) |
| a/T_h | 0.055 | 0.074 | 0.105 | 0.071 |
| R_2 | 0.945 | 0.969 | 0.950 | 0.941 |

T_h = handling time; a = successful attack rate (measure of searching efficiency)

Table 3
Functional responses of *Phytoseius plumifer* females (The mean number of prey eaten/day/female±SE) on different densities of *Tetranychus urticae* nymphal stages at different temperatures (n=14)

| Prey density | 15°C | 20°C | 25°C | 30°C |
|--------------|---------------|-------------|------------|------------|
| 2 | 1.50±0.5a | 1.64±0.4a | 1.78±0.4a | 1.71±0.4a |
| 4 | 2.21±0.8b | 2.21±0.6b | 3.35±0.8a | 2.92±0.9a |
| 8 | 4.78±1.1a | 5.14±0.8a | 5.78±1.1a | 5.42±1.8a |
| 16 | 5.28±0.6c | 8.07±1.4b | 10.78±2.6a | 8.50±2.3b |
| 32 | 13.00±3.7 b c | 14.57±3.3ab | 16.21±4.8a | 11.50±2.6c |
| 64 | 20.28±4.2b | 23.46±3.6a | 24.64±4.8a | 23.14±4.9a |

Different letters (a, b and c) in each row show the significant differences between among means ($P < 0.01$, LSD).

of *P. plumifer* were estimated using Rogers's equation and increased with temperature from 15°C (0.020, 0.492) to 25°C (0.059, 0.651) but declined at 30°C (0.030, 0.425) respectively. An unavoidably long handling time can be compensated for by a long searching period (Hassell 1977). Handling rates (T/T_h) ranged from 48.8 prey day⁻¹ at 15°C to 56.5 prey day⁻¹ at 30°C. The highest handling rate was observed at 30°C (56.5 prey day⁻¹). Judging by the a/T_h values, the predatory mite *P. plumifer* was most efficient against *T. urticae* at 20–30°C. Summary statistics for all assays are given in Table 2.

At all prey densities, prey consumption increased as the temperature increased from 15 to 25°C, except at 30°C, at which it decreased slightly. Data analysis indicated that there were significant differences between eaten preys at different temperatures in prey densities (Table 3).

Effect of temperature on prey consumption of immature stages of *P. plumifer*.

The number of prey consumed daily by the protonymphal stage increased with temperature from 0.71 (15°C) to 2.37 (25°C). The prey consumption decreased from 1.98 to 1.92 preys at 30 to 35°C, respectively and then increased again (4.25 preys at 37°C).

The daily prey consumption of the deutonymphs ranged from 1.30 to 5.46 prey/day at 15 to 35°C, respectively; however it decreased to 3.60 prey/day at 37°C. The daily prey consumption of the nymphal stages increased with temperature from 2.01 to 7.88 (prey/day) at 15 to 37°C (Table 4).

The total prey consumption of the protonymphs increased with temperature from 3.97 (15°C) to 5.44 (25°C). The total number of prey consumed by the two nymphal stages (protonymph and deutonymph) decreased as the temperature increased from 15.41, 19.38 (15°C) to 1.64, 5.24 (30°C), and then increased again (Table 5).

Effect of temperature on prey consumption of *P. plumifer* females. The daily prey consumption of pre-ovipositing and ovipositing females increased as the temperature increased. The daily prey consumption for post-ovipositing females and females in the whole life time increased as the temperature increased from 2.61, 8.85 (15°C) to 10.92, 24.89 (25°C), and then decreased at higher temperatures (Table 4).

The total amount of prey consumed by pre-ovipositing females decreased with temperature (15 to 30°C); the prey consumption decreased at the temperatures from 35 to 37°C. The total prey

Table 4

Effect of different temperatures on daily prey consumption of different life stages of *Phytoseius plumifer* on *Tetranychus urticae* (The mean number of prey eaten/day/different life stages \pm SE)

| Daily prey consumption of different stages | 15°C | 20°C | 25°C | 30°C | 35°C | 37°C |
|--|-----------------|-----------------|------------------|------------------|------------------|------------------|
| Protonymph | 0.71 \pm 0.3d | 1.12 \pm 0.6d | 2.37 \pm 0.8b | 1.98 \pm 0.5bc | 1.92 \pm 0.7c | 4.25 \pm 0.8a |
| Deutonymph | 1.30 \pm 0.4d | 1.49 \pm 0.6d | 2.18 \pm 0.9c | 2.40 \pm 0.8c | 5.46 \pm 1.7a | 3.60 \pm 1.0b |
| Nymphal stages | 2.01 | 2.61 | 4.55 | 4.38 | 7.38 | 7.88 |
| Pre-oviposition | 3.17 \pm 0.8c | 3.25 \pm 0.8c | 3.44 \pm 0.5c | 5.46 \pm 1.8b | 6.76 \pm 1.4b | 10.80 \pm 4.2a |
| Oviposition | 3.07 \pm 0.7d | 5.62 \pm 1c | 10.53 \pm 1.6b | 10.11 \pm 1.5b | 15.11 \pm 3.0a | 9.35 \pm 2.0b |
| Post-oviposition | 2.61 \pm 0.9d | 3.53 \pm 1.1d | 10.92 \pm 3.9a | 5.42 \pm 0.8c | 9.94 \pm 1.9ab | 8.75 \pm 1.5b |
| Female prey consumption | 8.85 | 12.40 | 24.89 | 20.99 | 31.81 | 28.90 |

Different letters (a, b and c) in each row show the significant differences between among means ($P < 0.01$, LSD).

Table 5

Effect of different temperatures on total prey consumption of different life stages of *Phytoseius plumifer* on *Tetranychus urticae* (The mean number of prey eaten/female, \pm SE)

| Total prey consumption of different stages | 15°C | 20°C | 25°C | 30°C | 35°C | 37°C |
|--|---------------------|---------------------|--------------------|---------------------|---------------------|--------------------|
| protonymph | 3.97 \pm 0.4 c | 4.04 \pm 0.3c | 5.44 \pm 0.6b | 3.60 \pm 0.2c | 1.91 \pm 0.2d | 9.70 \pm 1.4a |
| Deutonymph | 15.41 \pm 0.8a | 8.78 \pm 0.6c | 4.23 \pm 0.4d | 1.64 \pm 0.2e | 5.30 \pm 0.5d | 10.09 \pm 1.9b |
| Nymphal stages | 19.38 \pm 0.9a | 12.82 \pm 0.7b | 9.67 \pm 0.6c | 5.24 \pm 0.3e | 7.21 \pm 0.5d | 19.79 \pm 3.2a |
| Pre-oviposition prey consumption | 42.33 \pm 3.6a | 15.35 \pm 1.6c | 6.45 \pm 0.9d | 5.26 \pm 0.8d | 9.25 \pm 1.9cd | 29.00 \pm 7.9b |
| Oviposition prey consumption | 114.27 \pm 14.6cd | 158.73 \pm 14bc | 238.32 \pm 33.7a | 205.84 \pm 23.5ab | 206.00 \pm 25.4ab | 42.00 \pm 18.3d |
| Post-oviposition prey consumption | 61.70 \pm 14.2cd | 104.00 \pm 23.5cd | 182.21 \pm 52.6a | 122.00 \pm 9.3abc | 164.91 \pm 26.2ab | 42.33 \pm 7.2d |
| Female | 218.30 \pm 13.6c | 278.08 \pm 16.9bc | 426.98 \pm 22.9a | 333.10 \pm 20.1bc | 380.16 \pm 38ab | 113.33 \pm 12.4d |

Different letters (a, b and c) in each row show the significant differences between among means ($P < 0.05$, LSD)

consumption during the oviposition period, the post-oviposition period and the total female prey consumption increased as the temperature rose from 15 to 25°C and then decreased at higher temperatures (Table 5).

DISCUSSION

A type II (the proportion of preys consumed declines monotonically with prey density) was observed in most studies involving predatory arthropods, including those on phytoseiid mites such as *P. plumifer*. The type II functional response model is most typical for predatory mites from phytoseiids such as protonymphs and deutonymphs of *Phytoseiulus persimilis* Athias-Henriot feeding on protonymphs of *Tetranychus pacificus* McGregor (Eveleigh and Chant 1981) and eggs of *T. urticae* (Fernando and Hassell 1980; Takafugi and Chant 1976). It was observed for the adult female of *P. persimilis* when feeding on the eggs of *T. urticae*

(Skirvin and Fenlon 2003). The same results were reported for adult females of *Phytoseiulus longipes* Evans when fed on adults and different active immature stages of *Aponychus corpuzae* Rimando and *T. pacificus* (Badii et al. 1999). It was also reported that the type II functional response was observed in *Typhlodromus bambusae* on *Schizotetranychus narjngensis* Ma et Yuan females, *Amblyseius longispinosus* Evans on adult females of *Aponychus corpuzae* Rimando (Zhang et al. 1998, 1999), *Amblyseius californicus* McGregor (Gotoh et al. 2004) and *Typhlodromus kettanehi* Dosse (Shirdel et al. 2004) fed on different densities of eggs, larvae and adult males and females of *T. urticae*. The results of above-mentioned literature revealed that type II functional response is very common among phytoseiid species.

The total prey consumption of the protonymph, deutonymph and female of the examined phytoseiid at 25°C in our study was 5.44, 4.23 and

426.98 specimens of *T. urticae*, respectively, that was near to values obtained by Zaher et al. (1969), (6.3, 15.6 and 412 specimens of *T. cinnabarinus* at 27°C). The difference was due to different life stages of the prey, temperature and the presence of pollen. They also mentioned that development was more rapid when *P. plumifer* was fed on different active stages of red spider mites (*Tetranychus cinnabarinus*) than on their eggs or adults. They concluded that an increase in temperature has a positive effect on prey consumption until the optimal temperature is reached, and then the effect of temperature becomes negative.

The daily prey consumption of deutonymph and protonymph stages increased as the temperature increased, whereas the total prey consumption decreased as the temperature increased. Development time was also affected by temperature: the time for development increased as the temperature decreased. Low temperatures caused an increase in developmental time, which resulted in an increase in the total prey consumption.

Comparing data on the functional response at the highest density and on the daily prey consumption of *P. plumifer* at the same temperatures revealed that the functional response at all temperatures except 25°C was higher than the daily prey consumption. In the prey consumption experiment, *P. plumifer* fed on corn pollen in addition to *T. urticae* that they were commensurate.

Our study showed that the highest total prey consumption and searching efficiency of *P. plumifer* was at 25 °C.

CONCLUSION

Results of this study agree with other studies that concluded the amount of attack rates, handling time and predation increased as temperature increased at around 20 to 30 °C. The laboratory results presented in this study suggest that *P. plumifer* could be considered as a useful agent on two spotted spider mite *T. urticae* for a biological control in greenhouses and outdoor settings at temperatures in the range from 20 to 30 °C.

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