



## Prey consumption and functional response of a phytoseiid predator, *Neoseiulus womersleyi*, feeding on spider mite, *Tetranychus macfarlanei*

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### Abstract

The spider mite, *Tetranychus macfarlanei* (Baker and Pritchard) (Acari: Tetranychidae) is a pest of various crops and trees with a cosmopolitan geographic range that includes the country of Bangladesh. This study was conducted to evaluate the biological control potential of the predacious mite, *Neoseiulus womersleyi* (Schicha) (Acari: Phytoseiidae), against *T. macfarlanei*. The consumption rate (when offered egg, larvae, protonymph, and deutonymph as prey) and functional responses (over different prey densities) of *N. womersleyi* were investigated in laboratory experiments. Experimental results showed that the predator consumed significantly more larvae than other stages of *T. macfarlanei*. Logistic regression indicated that the predator exhibited a Type II functional response on all immature stages of prey; the number of prey consumed increased with prey density up to a maximum after which it slowly decreased. The attack rate ( $a$ ) and handling time ( $T_h$ ) coefficients of a Type II response were estimated by fitting Holling's disc equation to the data. The lowest estimated value of  $a$  and the highest value of  $T_h$  were obtained for the predator feeding on deutonymphs. The lowest value of  $T_h$  was obtained for the predator feeding on larvae. However, the attack rate on larvae was not significantly different than the attack rate obtained on eggs and protonymphs. The predicted maximum daily prey consumption was 212.8 eggs, 238.1 larvae, 53.5 protonymphs, and 29.6 deutonymphs. Thus, our results suggest that *N. womersleyi* could be a highly efficient biological control agent of *T. macfarlanei* at least at low prey densities, although field studies are needed to draw firm conclusions.

**Keywords:** biological control, prey consumption

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## Introduction

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Phytophagous mites are becoming more aggressive as pests on vegetable crops due to environmental changes and cropping systems. In general, tetranychid mites are harmful and widespread pests on numerous crops and ornamental plants (Kasap and Atlihan 2011). *Tetranychus macfarlanei* (Baker and Pritchard) (Acari: Tetranychidae) is one of the most common spider mite pests of vegetables, fruits, forests, and ornamental plants in the world. It attacks crops of the family of Convolvulaceae, Cucurbitaceae, Fabaceae, Malvaceae and Solanaceae (Jeppson et al. 1975), which includes bananas, beans, cotton, cucumber, eggplant, melons, okra, papaya, peanut, watermelon, and ornamentals. It occurs in Bangladesh, India, Madagascar, Mauritius, Thailand, Japan, Taiwan, USA, Malayasia, and the Canary Islands (personal communication). In Bangladesh, *T. macfarlanei* is a dominant spider mite pest that infests many important agricultural crops such as jute, bean, and cucumber, and is found throughout most of the country.

Presently, control of this mite pest depends mainly on chemical applications. However, the intensive application of miticides in combination with short life cycles and high reproductive rates has led to the evolution of resistance to miticides. Most of the recent research on biological control of tetranychids has focused on the family Phytoseiidae, due to their frequent effectiveness in maintaining prey populations at low densities (McMurtry and Croft 1997; Croft and Luh 2004; Broufas et al. 2007). The phytoseiid mite, *Neoseiulus womersleyi* (Schicha) (Acari: Phytoseiidae) is an important natural enemy of the Kanzawa spider mite, *Tetranychus kanzawaki* Kishida (Acari: Tetranychidae) in tea fields (Hinomoto

et al. 2011). *N. womersleyi* is one of the most important predators of spider mites of the genus *Tetranychus* in Japan (Maeda and Hinomoto 2006). It was reported that *N. womersleyi* suppressed populations of dominant spider mites such as *T. kanazawai* and *T. urticae* Koch at low prey densities (Mori and Saito 1979; Hamamura 1986). *N. womersleyi* also suppressed a dominant spider mite, *T. macfarlanei*, in Bangladesh (personal observation), but no detailed information is available on predator-prey interactions.

The functional response concept was first described by Holling (1959) and has been widely utilized to evaluate effectiveness of predators (Laing and Osborn 1974; Everson 1980; Sabelis 1985; Trexler et al. 1988; De Clercq et al. 2000; Badii et al. 2004; Reis et al. 2003, 2007; Timms et al. 2008). The rate at which predators attack prey is to some extent dependent on prey density. This relationship has been defined as the functional response (Solomon 1949). It is one of the most important aspects of a predator-prey relationship and a major parameter of population models (Berryman 1992). It has been used to predict mechanisms underlying predator-prey dynamics and to predict the potential effectiveness of candidates for biological control (Sepúlveda and Carrillo 2008). The functional response can determine if a predator is able to regulate the density of its prey (Murdoch and Oaten 1975), i.e., it must show density dependence; the predator must respond to higher prey densities by consuming an increasing proportion of the available prey over a range of prey densities (Schenk and Bacher 2002).

Despite the potential of *N. womersleyi* for tetranychid control, no information is available about its predator-prey interactions

with *T. macfarlanei*. This information is essential to predict the efficiency of *N. womersleyi* as a biological control agent of spider mites, and in particular for tetranychid mites. The present study was designed to compare the consumption rate and functional responses of *N. womersleyi* feeding on different stages of *T. macfarlanei*. The following questions were addressed: (i) does the feeding rate of the predator vary among different stages of same prey species?; (ii) are functional responses different among different stages of the same prey?; (iii) what is the potential of this predator for biological control of *T. macfarlanei* populations?

## Materials and Methods

### Stock cultures of mites

The stock culture of *N. womersleyi* was maintained using all stages of *T. urticae* on common bean leaves, *Phaseolus vulgaris* L. (Fabales: Fabaceae), in a rearing chamber ( $25 \pm 2$  °C,  $65 \pm 10\%$  RH and 16:8 L:D). Leaves were placed upside-down on a layer of filter paper placed on a polystyrene pad (2 cm thick) saturated with tap water. This set-up was placed in a plastic box ( $20.9 \times 15 \times 9.5$  cm) to which water was added daily to keep the filter paper and polystyrene pad wet, and to cover the base of the box to prevent the mites from escaping. A surplus of all stages of *T. urticae* was brushed daily onto the leaf by using a soft brush and funnel. Leaf discs were renewed as necessary. The predatory mites used in the experiment were reared for at least three consecutive generations prior to this study. The spider mite *T. macfarlanei* was cultured on leaf discs ( $\sim 12$  cm<sup>2</sup>) of *P. vulgaris* placed on a water-saturated polyurethane mat in a Petri dish (9 cm diameter) at  $25 \pm 2$  °C under a 16:8 L:D photoperiod (Gotoh et al. 2006).

### Experimental conditions

All experiments were carried out at  $25 \pm 1$  °C,  $65 \pm 10\%$  RH and 16:8 L:D photoperiod. Reproductively active females of *N. womersleyi* were used in all experiments. Before each test, the predators were placed individually in Petri dish (9 cm diameter) and starved for 24 hours. The leaf discs were surrounded with strips of wet filter paper in order to minimize the escape of individual mites. Individuals trapped in the wet filter paper surrounding the leaf discs were excluded from data analysis.

### Prey consumption

To assess consumption rates on different life stages, 100 newly emerged individual eggs, larvae, protonymphs, and deutonymphs of *T. macfarlanei* were offered as food. After 24 hours, the number of individuals consumed was recorded by counting intact or living prey stages (Gotoh et al. 2004b). 15 to 20 replicates were conducted for each prey life stage.

### Functional response

Functional response experiments were also carried out in Petri dishes with a leaf arena of 4 cm<sup>2</sup>. Once again, reproductively active, gravid females were used. The experiments were conducted with seven densities (5, 10, 20, 40, 50, 70, and 100 newly-emerged individuals) of different prey stages (egg, larvae, protonymph, and deutonymph). Prey mites were transferred onto leaf discs with a fine soft brush and then a single predator (starved for 24 hours) was released into the dish. After 24 hours, the predators were removed and the number of consumed or/and killed prey was counted. Individuals injured during transfer were excluded from analysis. After 24 hours, the number of prey items consumed was recorded by counting intact or living prey that remained. For each prey life stage 15 to 20 replicates were conducted.

### Data analysis

The influence of prey stage on consumption rate of the predator was analyzed by one-way ANOVA and means were compared separated using the Tukey's Honestly Significant Difference test (SPSS 2008). Values were ln-transformed (consumption rate) for analysis. 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 of *N. womersleyi* to different stages of *T. macfarlanei* because of difficulties in discriminating between Holling's (1966) Type II and Type III (Trexler et al. 1988; Juliano 2001). The data were fitted to a polynomial function that described the relationship between the proportion of prey consumed and initial density:

$$N_e/N_0 = \sqrt{(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)} + \sqrt{(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)} \quad (1)$$

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 of the intercept, linear, quadratic, and cubic coefficients respectively. The equation 1 was transformed to:

$$\ln(N_e/(N_0 - N_e)) = P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3 \quad (2)$$

The values of  $P_0$ ,  $P_1$ ,  $P_2$  and  $P_3$  were estimated by using a cubic mathematical function for curve estimation (Table 2).

The type of functional response was determined by fitting data to the logistic regression model; the sign of  $P_1$  and  $P_2$  were used to distinguish the shape of the curves. When the function is negative (linear coefficient  $< 0$ ), the predator displays a Type II functional response that indicates the

proportion of prey consumed declines monotonically. When a density-dependent result for the proportion of prey consumed is positive (linear coefficient and quadratic coefficient  $> 0$ ), the predator is said to display a Type III functional response (Juliano 2001).

The handling time ( $T_h$ ) and the attack constant ( $\alpha$ ) were estimated using Holling's disc equation modified by reciprocal linear transformation (Livdahl and Stiven 1983). The modified equation is as follows:

$$N_e = \alpha TN_0 / (1 + \alpha T_h N_0) \quad (3)$$

where  $N_e$  = the number of prey attacked,  $T$  = exposure time (1 day),  $\alpha$  = attack rate, a constant rate of successful search, and  $T_h$  = handling time. Equation 3 was transformed to:

$$1/N_e = T_h/T + 1/(\alpha TN_0) \quad (4)$$

where  $1/N_e$  represents  $y$ ,  $N_0$  represents  $x$ ,  $T_h/T$  represents  $a$ , and  $1/(\alpha T)$  represents  $b$ . Then, the regression form became  $\underline{y} = a + bx$ . The values of  $\alpha$  and  $T_h$  were estimated by using an inverse mathematical function for curve estimation. Then, the maximum number of consumed prey per predator (asymptote)  $Na_{max} = T/T_h$  was found.

The effect of prey stage on the attack rate ( $\alpha$ ) and handling time were analyzed by one-way ANOVA using Tukey's Honestly Significant Difference test (SPSS 2008) with values ln-

**Table 1.** Mean consumption rate  $\pm$  SE of *Neoseiulus womersleyi* feeding on *Tetranychus macfarlanei*: mean consumption and proportion of prey consumed ( $N_e/N_0$ ;  $N_0$  is initial density,  $N_e$  is number of prey attacked).

Prey stage	No. of prey consumed	$N_e/N_0$
Egg	62.25 $\pm$ 4.39b	0.62b
Larvae	69.87 $\pm$ 3.61a	0.69a
Protonymph	31.87 $\pm$ 1.19c	0.32c
Deutonymph	23.81 $\pm$ 0.96d	0.24d
Df=63, F-value <sup>a</sup>	103.859**	1.463E3**

<sup>a</sup>Data were analyzed using ANOVA; \*\*  $p < 0.001$ ; values within the columns followed by the different letter were significantly different at 0.1% level (Tukey's Honestly Significant Difference test).

**Table 2.** Maximum likelihood estimates from logistic regression of proportion of prey consumed as a function of initial prey densities by adults of *Neoseiulus womersleyi*.

Prey stage	Model summary					Parameter estimates			
	$R^2$	F-value	df 1	df 2	p	$P_0$	$P_1$	$P_2$	$P_3$
Egg	0.317	10.22	3	66	0.000	1.300	-0.087	0.002	1.353E+05
Larvae	0.158	3.946	3	63	0.012	0.930	-0.004	0.000	1.559E+06
Protonymph	0.659	43.784	3	68	0.000	4.512	-0.177	0.002	-1.020E+05
Deutonymph	0.810	102.347	3	72	0.000	2.987	-0.095	0.000	1.470E+06

**Table 3.** Mean values ( $\pm$  95% confidence intervals) of search rate and handling time for *Neoseiulus womersleyi* feeding on *Tetranychus macfarlanei* (egg, larva, protonymph, and deutonymph).

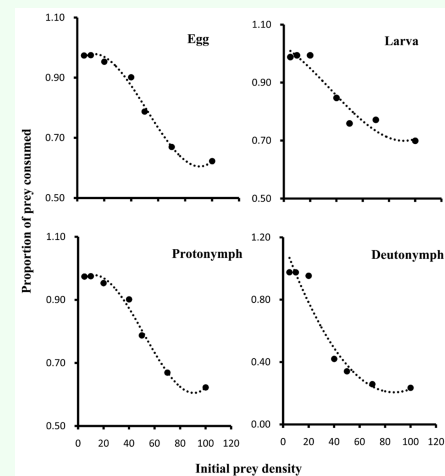
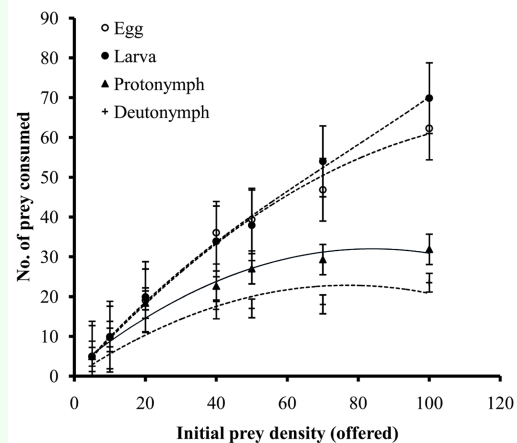
Prey stage	Attack rate ( $\alpha$ ) $\pm$ SE	Handling time ( $T_h$ ) $\pm$ SE	Predicted maximum predation rate	$R^2$
Egg	1.004 $\pm$ 0.001a	0.0047 $\pm$ 0.00b	212.77	0.99
Larva	1.016 $\pm$ 0.001a	0.0042 $\pm$ 0.00a	238.09	0.99
Protonymph	1.133 $\pm$ 0.001b	0.0187 $\pm$ 0.00c	53.48	0.99
Deutonymph	1.236 $\pm$ 0.002c	0.0338 $\pm$ 0.00d	29.59	0.95
df = 63, F-value <sup>a</sup>	1.156E4***	7.858E4***		

<sup>a</sup>Data were analyzed using ANOVA; \*\*  $p < 0.001$ . Values within the columns followed by the same letter were not significantly different at 5% level (Tukey's Honestly Significant Difference test).

transformed prior to analysis.

## Results

The life stage of *T. macfarlanei* had an effect on the mean consumption rate of *N. womersleyi* (Table 1). Larvae were the most consumed prey type, followed by egg, protonymph, and deutonymphs, respectively (Table 1). The percentage of prey consumed for each prey stage declined with increasing prey density (Figure 1), implying inverse density-dependence, and the logistic regression for all prey stages had a significant linear parameter ( $P_1 < 0$ ) and positive quadratic coefficient, suggesting that the predator displayed a Type II response on all four life stages. Thereafter, Holling's disc equation was used to estimate the attack rate coefficient ( $\alpha$ ) and the handling time ( $T_h$ ); these parameters illustrated this relationship numerically (Table 3). The negative values obtained for the linear parameters ( $P_1 < 0$ ) and inverse density-dependence relationship between the proportion of prey consumed and the initial prey density on all prey stages tested were all consistent with a Type II response.

**Figure 1.** Mean proportion ( $\pm$ SE) of prey consumed by adult females of *Neoseiulus womersleyi* at five densities of *Tetranychus macfarlanei*. High quality figures are available online.**Figure 2.** Functional response of adult females of *Neoseiulus womersleyi* feeding on different stages of *Tetranychus macfarlanei*. Points show average number of individuals consumed or killed by the predator at each level of initial prey density. High quality figures are available online.

Functional response curves revealed that the predators responded more vigorously at lower densities of all stages of *T. macfarlanei* (Figure 2). Similar consumption rates were obtained on eggs, larvae, and deutonymphs at the density of 10 prey/day, but the consumption rate of larvae was significantly higher than on other life stages at the highest density. The attack rate coefficient ( $\alpha$ ) was lowest for the predator feeding on deutonymphs, whereas those obtained on other prey stages (egg, larva) were similar, given overlapping confidence intervals (Table 3). Handling time ( $T_h$ ) varied significantly among life stages with the shortest  $T_h$  obtained on larvae, followed by eggs, protonymphs, and deutonymphs.

## Discussion

To our knowledge, this is the first test of the predation potential of *N. womersleyi* when offered *T. macfarlanei* as prey. The consumption rate of the predator was generally inversely related to the size of the life stage, although consumption of larvae was higher than that of eggs. Although the larva is slightly bigger than the egg, eggs and larvae of *T. urticae* provide similar nutritional benefits to predators (Ohnesorge 1981; Sabelis 1985). The higher consumption rate on larvae might be due to the fact that larvae feed in clusters that make them easier prey, although larvae were released onto bean leaf discs in a scattered form. Higher consumption rates on larvae compared to eggs were reported for *Kampimodromus aberrans* feeding on *T. urticae* (Kasap an Altihan 2011). Another possibility is that the mouthparts of *N. womersleyi* may be more effective in piercing larvae than the egg chorion. It is also reported by Blackwood et al. (2001) that generalist species may have mouthparts that are not as effective in piercing

the egg chorion of *T. urticae* as mouthparts of more specialized species.

Previous studies in which related phytoseiid species were evaluated on *T. urticae* have produced contrasting results (Burnett 1971; Takafuji and Chant 1976; Blackwood et al. 2001, 2004). Blackwood et al. (2001) reported that generalist predators showed no prey-stage preference or preferred larvae when offered *T. urticae* as prey. *Phytoseiulus macropilis*, *P. persimilis*, *Neoseiulus longispinosus*, and *N. fallacies* preferred eggs to the larvae. *Kampimodromus aberrans*, *Galendromus occidentalis*, *N. barkeri*, *N. californicus*, *N. cucumeris*, and *Typhlodromus pyri* showed no prey-stage preference. *Amblyseius andersoni*, *Euseius finlandicus* and *E. hibisci* preferred larvae to eggs.

Predacious mites in the family Phytoseiidae can be classified into four categories based on their feeding habits and related biological and morphological traits (McMurtry and Croft 1997). Type I phytoseiids (e.g., *Phytoseiulus* spp.) are specialized predators of spider mites, *Tetranychus* spp. Type II phytoseiids are selective predators of *Tetranychus* species. Examples include *Galendromus* spp. and some *Neoseiulus* spp. Type III phytoseiids (e.g., *Amblyseius* spp.) are generalist predators, while Type IV phytoseiids (e.g., *Euseius* spp.) are specialized pollen feeders/generalist predators. Thus, *N. womersleyi* fitted a Type II response for *T. macfarlanei*. The functional response of other phytoseiid species such as *E. hibisci* (Badii et al. 2004), *P. persimilis*, *G. occidentalis*, *N. californicus* (Xiao and Fadamiro 2010), and *K. aberrans* (Kasap an Altihan 2011) also fit a Type II response.

Functional response curves showed that the proportions of prey consumption by *N.*

*womersleyi* were higher at lower densities for all stages of *T. macfarlanei*. A significant decline in consumption rate at higher prey densities is most likely due to satiation (Mills 1982). This pattern indicates that *N. womersleyi* would be more effective at controlling *T. macfarlanei* populations at lower densities, and that the predator would need to be released early and before *T. macfarlanei* reached high densities.

The coefficient of attack rate and handling time are parameters used to determine the magnitude of functional responses (Pervez and Omkar 2005). The lowest attack rate coefficients ( $\alpha$ ) were obtained on deutonymphs, and values obtained for other life stages were significantly different. This indicates that attack rates varied among different densities of egg, larva, and protonymph, possibly because consumption rates on these prey stages were dissimilar. Similarly, Kasap and Altihan (2011) found that feeding different densities of *T. urticae* eggs, larvae, and protonymphs by *K. aberrans* did not change the attack rate coefficient although it did change when feeding on deutonymphs.

Handling time is a good indicator of consumption rate and predator efficacy because it reflects the cumulative time required to capture and kill the prey (Veeravel and Baskaran 1997). Different factors may influence the handling time of natural enemies, e.g., the speed of predator and prey movement and the time spent subduing a prey individual (Hassell 1978), which again may relate to both behavioral and structural prey defense mechanisms. Handling time coefficients varied among life stages of *T. macfarlanei* and in general decreased as prey size was reduced. But the value obtained on larvae was lower than that obtained on the

eggs. Again, this may be due to the fact that the predator was not successful in piercing the egg chorion, as is the case for other generalist phytoseiid predators such as *A. andersoni*, *E. finlandicus*, and *E. hibisci* (Blackwood et al. 2001). Similarly, Kasap and Altihan (2011) reported that *K. aberrans* had a lower handling time on larvae than on eggs when consuming *T. urticae*. On the other hand, significant variation in the estimates of handling time of *N. womersleyi* on different stages of *T. macfarlanei* indicates that any one component of the handling time might have been positively affected when larvae were used as prey rather than another life stage. For generalist phytoseiid mite species, there is some evidence that suggests spider mite larvae may be more profitable than eggs with regard to handling time (Blackwood et al. 2001).

In conclusion, our results suggest that *N. womersleyi* has the potential to serve as a biological control agent of *T. macfarlanei* at low density, so any augmentative field releases of the predator should be undertaken before high densities of *T. macfarlanei* are reached. Apart from the functional response, factors such as intrinsic rate of increase, host distribution, intraguild predation and competition, host plant effects, and various abiotic environmental factors can have important impacts on the efficiency of predators in regulating a prey population. Thus, although these controlled laboratory studies provide some insight into the predator-prey interaction, field studies are required for more conclusive estimation of biocontrol potential and the development of better management tactics for the control of *T. macfarlanei*.

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