Functional and numerical responses of Amblydromalus limonicus and Neoseiulus cucumeris to eggs and first instar nymph of tomato/potato psyllid (Bactericera cockerelli)

Authors: Patel, Kajal, and Zhang, Zhi-Qiang

Source: Systematic and Applied Acarology, 22(9) : 1476-1488

Published By: Systematic and Applied Acarology Society

URL: https://doi.org/10.11158/saa.22.9.12

Systematic & Applied Acarology 22(9): 1476–1488 (2017)
http://doi.org/10.11158/saa.22.9.12

ISSN 1362-1971 (print)
ISSN 2056-6069 (online)

Article

Functional and numerical responses of *Amblydromalus limonicus* and *Neoseiulus cucumeris* to eggs and first instar nymph of tomato/potato psyllid (*Bactericera cockerelli*)

KAJAL PATEL[1] & ZHI-QIANG ZHANG[1, 2]
[1]*School of Biological Sciences, the University of Auckland, Auckland, New Zealand*
[2]*Landcare Research, 231 Morrin Road, Auckland, New Zealand;*
author for correspondence: ZhangZ@landcareresearch.co.nz

Abstract

The tomato/potato psyllid (TPP), *Bactericera cockerelli*, is a serious pest of some agricultural and ornamental plants, especially of the Solanaceae family. It has been an invasive species in New Zealand since 2006, heavily impacting the potato and tomato industry. The functional and numerical responses of the phytoseiid predators *Amblydromalus limonicus and Neoseiulus cucumeris* were examined by offering a range of prey densities (two, four, eight, 12, 16, 20, 24 and 28 TPP eggs or 1st instar nymphs) and compared on a capsicum leaf disc under 25 ± 1ºC, 85% ± 5% RH and a 14:10 h light: dark (L:D) photoperiod. Both species displayed a type 2 functional response when fed on eggs or 1st instar nymphs of TPP, indicating an increase in the number of prey killed with an increase in prey population density. The results were analysed by using a logistic regression and Holling disc equation. *A. limonicus* had a higher attack rate for both eggs (0.05 ± 0.01) and 1st instar nymphs (0.06 ± 0.01) than *N. cucumeris*, which had an attack rate of (0.03 ± 0.01) for eggs and (0.02 ± 0.01) for 1st instar nymphs of TPP. *N. cucumeris* had a longer handling time for both eggs (3.68 ± 0.67 hrs) and 1st instar nymphs (2.50 ± 0.79 hrs) compared with *A. limonicus*, with a handling time of (1.74 ± 0.23 hrs) for eggs and (1.15 ± 0.15 hrs) for 1st instar nymphs. *A. limonicus* consistently produced significantly more eggs than *N. cucumeris* across all densities when fed on either eggs or 1st instar nymphs of TPP. However, the results showed the lack of numerical response of both predator species to prey density. The stronger functional response of *A. limonicus* to TPP eggs and 1st instar nymphs indicates that this species can potentially be a more effective biocontrol agent of TPP than *N. cucumeris*.

Key words: Biological control, psyllids, invasive insects, predatory mites, predation, functional response, numerical response

Introduction

Food webs are descriptive devices defined by the linkages between consumers and their resources (Kratina *et al.* 2009). The food web systems are complex and intrinsically dynamic (Kratina *et al.* 2009). In predator-prey interaction, a predator's performance is dependent on numerous characteristics, two of which are the numerical response and functional response (Rahman *et al.* 2012; Juliano 2001). These responses provide data on the biocontrol efficiency of a natural enemy against a particular pest (Rahman *et al.* 2012; Juliano 2001).

The functional response describes the relationship between an individual's consumption rate and food density (Rahman *et al.* 2012; Solomon 1949). Three types of functional responses were described by Holling (1959a, 1959b, 1961). The type 1 response is the linear response where the number of prey killed increases linearly to a maximum, and then remains constant as prey density increases. In the type 2 response, the number of prey consumed increases with prey density at a decelerating rate towards an asymptote. A type 3 response, the sigmoid response, depends greatly on the experimental conditions and the feeding history of the predator. While arthropods exhibit both type 2 and 3 responses, type 2 is observed most often (Cedola *et al.* 2001). The basic factors that affect functional response are: food identification, search rate, capture, prey consumption, and time of exposure of predator to prey (Holling 1959b). Functional response is an important factor in the dynamics of a predator-prey relationship and is a key component of a population model (Sepulveda & Carillo 2008). It has been used to forecast the mechanisms underlying predator-prey behaviour to improve the practical predictive potential of predator candidates for biocontrol. The numerical response is the change in a predator's reproductive output at varying prey densities (Rahman *et al.* 2012; Juliano 2001; Hassell 1978).

The tomato/potato psyllid (TPP), *Bactericera cockerelli*, is a serious pest of some agricultural and ornamental plants, especially of the Solanaceae family (Butler & Trumble 2012). An outbreak of TPP can result in significant plant damage such as defoliation, stunted growth, and reduced yield (Butler & Trumble 2012). A variety of TPP control methods are utilized around the world; however, most control of TPP populations depends heavily on pesticide application (Mauchline *et al.* 2013; Walker *et al.* 2015). Exploitation of natural enemies such as predatory mites is a potential way of minimizing pesticide usage as well as increasing the emphasis on environmentally friendly techniques of pest control.

Predatory mites from the family Phytoseiidae have been important biological control agents in the agriculture industry (McMurtry *et al.* 2013). These mites have been widely used in biological control programmes of several mites and small insect pests of fruits, vegetables, and other crop species worldwide (Opit *et al.* 2004; Arthurs *et al.* 2009; Juan-Blasco *et al.* 2012; McMurtry *et al.* 2013).

Amblydromalus limonicus and *Neoseiulus cucumeris* are type III generalist predatory mites and are relatively widely distributed (McMurtry *et al.* 2013). They can prey on a variety of small arthropods (e.g. whiteflies, scale insects, and mites) and can also feed on other food sources such as pollen across an extensive range of habitats (McMurtry *et al.* 2013). *A. limonicus* was first used against spider mites (*Oligonychus punicae* and *Tetrancyhus cinnabarinus*) in the USA in the 1960s (McMurtry & Scriven 1971). In the early 1990s, *A. limonicus* was used successfully to prevent and control the western flower thrips, *Frankliniella occidentalis* (Messelink *et al.* 2006). Recently, *A. limonicus* was commercialised and used in Europe primarily for thrips and whitefly control (Knapp *et al.* 2013; Medd & GreatRex 2014; Chorazy *et al.* 2016). In New Zealand, rates of predation of *A. limonicus* on TPP immature stages were reported at some fixed densities of prey (Xu & Zhang 2015; Davidson *et al.* 2016; Patel & Zhang 2017). However, there have been no studies determining the functional response of *A. limonicus* to a range of prey densities. In comparison, one of the top selling biocontrol agents worldwide is *N. cucumeris*, which is primarily used for controlling small insects such as thrips and phytophagous mites (Van Lenterten 2012). A type 2 functional response has been demonstrated for *N. cucumeris* against other prey species, e.g. *Thrips flavidulus* (Yao *et al.* 2014) and western flower thrips (Shipp & Whitfield 1991). However, no similar studies have been conducted on functional response of *N. cucumeris* to TPP.

This study is the second of a series of laboratory and greenhouse experiments to compare and evaluate the efficiency of two commercially available species of predatory mites (*A. limonicus* and *N. cucumeris*) as potential biocontrol agents of TPP. The first study (Patel & Zhang 2017) examined the preference of TPP eggs over 1st instar nymphs by *A. limonicus* and *N. cucumeris*. The results indicated that *N. cucumeris* can consume TPP eggs and 1st instar nymphs and that both predatory mites have the potential to consume more than 10 TPP eggs or 1st instar nymphs per day. Therefore, this study investigates the functional and numerical responses of *A. limonicus* and *N. cucumeris* to TPP. The aims of the study are to examine (a) how predation rates and reproductive rates of *A.*

limonicus and N. cucumeris increase with increasing densities of TPP eggs or 1st instar nymphs, and (b) if there is a difference in responses to prey density between the two predatory mite species.

Material and Methods

Insect and mite colonies

The colony of TPP in this study originated from greenhouse capsicums in south Auckland in 2012 (Xu & Zhang 2015) and was maintained on capsicum plants in a greenhouse at Landcare Research, Auckland (see Patel & Zhang 2017 for details).

The colony of *A. limonicus* used in the experiments were originally collected from greenhouse capsicums in south Auckland in 2012 and were kept and maintained in a cabinet environmentally controlled at 25 ± 1ºC, 85% ± 5% RH and a 14:10 h light:dark (L:D) photoperiod (Liu & Zhang 2017). The colony was maintained on *Typha orientalis* pollen (see Patel & Zhang 2017 for more details). The pollen was collected from a reserve in St Johns, Auckland and preserved at -18 ºC before use (Kar *et al.* 2015). The colony of *N. cucumeris* was purchased from BIOFORCE in South Auckland and was reared on *Tyrophagus putrescentiae* with bran (see Patel & Zhang 2017 for details).

Rearing of similar aged female predatory mites for experiments

Before the experiments were carried out, young females were standardised for age by rearing them from eggs of the same age. To obtain predator eggs of the same age, black fibrous strings (10mm), which served as microspace/oviposition sites for the predatory mites, were added to mite colonies to encourage oviposition. After 24 hours, eggs of *A. limonicus* and *N. cucumeris* were collected and reared on *T. orientalis* pollen in arenas as described in Patel & Zhang (2017). When *A. limonicus* and *N. cucumeris* adults emerged, males and females were paired for 2 days to ensure mating.

Experimental arenas used in tests

The experimental arena used in this study was modified from Munger cells of Liu & Zhang (2017) and described in detail in Patel & Zhang (2017). Briefly, the cells were made up of two transparent pexiglass slides: one was 38 mm x 38 mm which had a 16 cm diameter middle hole that served as a cell, and the other slide was 25 mm wide, 39 mm long, and 3mm thick (bottom piece). The cell was covered by a piece of cling film with small holes (punctured using a fine insect pin) to allow for ventilation. A capsicum leaf disc of 3 cm in diameter was used as an experimental substrate for the cell. To prevent desiccation, the leaf disc was placed upside down on moist filter paper kept in a zip plastic bag (9.5 mm x 6 mm) exposed to the cell bottom through a punctured hole (10.4 mm diameter). The plastic bag enabled the retention of water to keep the filter paper moist during the experiment. The top and bottom slides of the Munger cells were tightly clipped together to form an enclosed cell.

Functional and numerical tests

160 newly emerged pregnant females of *A. limonicus* and 160 newly emerged pregnant females of *N. cucumeris* were transferred individually into modified Munger cells. The predatory mites were starved for 24 hrs to standardise their level of hunger before use. After 24 h starvation, 80 *A. limonicus* and 80 *N. cucumeris* were placed individually onto a leaf disc presented with densities of TPP eggs or 1st instar nymphs of 2, 4, 8, 16, 20, 24, and 28. Each treatment contained 10 replicates. The same set up was conducted for the control experiment without the presence of a predatory mite. The tests were conducted for a 24-hr period. The number of eggs and 1st instar nymphs consumed,

and the number of predator eggs laid, were examined under a stereo-microscope. A predator was only tested once.

Statisitical analysis

A logistic regression of the proportion of prey consumed as a function of initial prey density was used to determine the shape of the functional repsonse curve of *A. limonicus* and *N. cucumeris* to different stages of TTP;

$N_e/N_o= \exp (P_o + P_1N_0 + P_2N^2_0 + P_3N^3_0) / 1 + \exp (P_o + P_1N_0 + P_2N^2_0 + P_3N^3_0)$

N_e is the number of prey consumed, N_o is the initial prey density, (N_e/N_o) is the probability of prey consumption and P_0, $P_{1,}$ $P_{2,}P_3$ are the maximum likelihood estimates of the intercept, linear, quadratic and cubic coefficients, respectively (Juliano 2001). To determine the type of functional response, the signs of P_1 and P_2 are used. The predator displays a type 2 response when the linear coefficient is significantly negative ($P_1 < 0$), which indicates that the proportion of prey consumed declines monotonically with the initial prey density. When the linear coefficient is positive ($P_1 > 0$), and the quadratic coefficient is negative ($P_2 < 0$), the predator has a type 3 functional response (Juliano 2001). The logistic regression analysis indicated that our data fit a type 2 functional response for eggs and 1st star nymphs of TTP for both predatory mite species; therefore, additional analyses conducted were restricted to a type 2 response.

A further analysis was conducted by carrying out non-least squares regression to estimate the attack rate (α) and handling time (T_h). The Holling disc model (Holling 1965) was used to model the relationship between numbers of prey consumed (N_e) and initial prey density (N_o):

$N_e= \alpha TN_o / (1 + \alpha T_hN_o)$

N_e is the number of prey consumed, N_0 is the initial prey density, α is attack rate, T is total predation time (1d = 24 hrs), and T_h is the handling time. Parameters with non-overlapping 95% confidence intervals were considered significantly different when parameters were compared across treatments.

All the analyses were performed using R Studio. The numbers of predator eggs laid on an egg or 1st instar diet across densities were compared using a two-way ANOVA. Analyses were carried out for both raw and log-transformed responsive variables and both displayed similar results. The results presented are from raw data only.

Results

Functional response

The interaction between predator species, density and prey stage was significant for the number of prey eaten (F=4.024; df=22; *P*=0.000). Thus the effects of predator species and prey density were analysed separately for eggs or 1st instar nymphs of TPP.

The interaction between predator species and TPP egg density was significant for the number of eggs eaten (*F*= 2.968; df=7; *P*=0.006), indicating different curves between the two species. The two curves overlapped initially at very low densities when both species could consume most of the prey provided, diverged gradually until the density of 16, and then diverged again after a short period of plateau between densities of 16 to 20 (Fig. 1). There was also a significant effect of density (F=19.047; df=7; *P*=0.000) and species (F=86.381; df=1; *P*=0.000) of the number of eggs eaten. *A. limonicus* consumed approximately twice the amount of eggs as did *N. cucumeris* across all densities except the lowest density of 2 (Table 1).

The interaction between predator species and prey density when the species were fed on 1st instar nymphs was significant for the number of prey eaten (F=5.763; df=7; *P*=0.000), indicating different curves between *N. cucumeris* and *A. limonicus*. The curves overlapped initially at very low densities when both species did eat most of the prey, diverged gradually until the density of 16, and then reached a plateau (Fig. 2). There was also a significant effect of density (28.698; df= 7; *P*=0.000) and species (158.975; df= 1; *P*=0.000) on the number of 1st instar nymphs eaten. At densities higher than 4, *A. limonicus* consumed more than twice the number of 1st instar nymphs than did *N. cucumeris* (Table 1).

TABLE 1. The number of prey consumed in 24 hours by each female of *A. limonicus* and *N. cucumeris* when presented with densities of 2, 4, 8, 16, 20, 24, or 28 eggs or 1st instar nymphs of TPP. Data in the format of mean ± s.e. (range). The number of replicates is 10 for each treatment.

Prey density	*A. limonicus*		*N. cucumeris*	
	Eggs of TPP	1st instar nymphs of TPP	Eggs of TPP	1st instar nymphs of TPP
2	1.4 ± 0.27 (0–2)	1.9 ± 0.10 (1–2)	1.4 ± 0.27 (0–2)	1.2 ± 0.25 (0–2)
4	3.9 ± 0.10 (3–4)	3.7 ± 0.21 (3–4)	1.8 ± 0.47 (0–4)	2.1 ± 0.38 (0–4)
8	5.7 ± 0.65 (2–8)	5.9 ± 0.48 (4–8)	3.0 ± 0.37 (2–5)	2.4 ± 0.40 (1–4)
12	7.0 ± 1.10 (1–12)	10.3 ± 0.40 (8–12)	3.0 ± 0.47 (1–5)	3.5 ± 0.86 (0–7)
16	9.7 ± 0.90 (5–14)	12.3 ± 0.73 (9–16)	5.2 ± 0.90 (2-11)	4.8 ± 0.84 (0–9)
20	8.2 ± 0.53 (6–11)	12.4 ± 1.03 (7–17)	4.4 ± 0.79 (1–10)	5.6 ± 0.88 (0–10)
24	8.7 ± 1.32 (2–17)	12.7 ± 1.53 (5–10)	5.0 ± 0.71 (3–10)	5.4 ± 1.11 (1–11)
28	10.2 ± 0.87 (6–16)	12.2 ± 1.03 (6–16)	4.4 ± 0.70 (2–9)	5.6 ± 1.10 (2–11)

TABLE 2. Maximum likelihood estimates from logistic regressions of the proportion of prey consumed as a function of initial TPP prey density by adult female *A. limonicus* and *N. cucumeris.*

	Prey Stage	Parameters	Estimate	SE	χ^2	*P* value
A.limonicus	Egg	Intercept (P_0)	-0.57508	0.06519	-8.821	< 0.0001
		Linear (P_1)	-2.85944	0.65511	-4.365	< 0.0001
		Quadratic (P_2)	-0.07553	0.58888	-0.128	0.898
		Cubic (P_3)	0.46934	0.51847	0.905	0.365
	1st Instar Nymph	Intercept (P_0)	-0.35338	0.06213	-5.688	< 0.0001
		Linear (P_1)	-2.10374	0.63031	-3.338	0.000845
		Quadratic (P_2)	-0.67549	0.55316	-1.221	0.222034
		Cubic (P_3)	-0.03007	0.47673	-0.063	0.949713
N.cucumeris	Egg	Intercept (P_0)	-1.19557	0.07783	-15.361	< 0.0001
		Linear (P_1)	-3.71593	0.76656	-4.848	< 0.0001
		Quadratic (P_2)	0.44439	0.70095	0.634	0.526
		Cubic (P_3)	-0.72116	0.63822	-1.130	0.258
	1st Instar Nymph	Intercept (P_0)	-1.14498	0.07746	-14.782	< 0.0001
		Linear (P_1)	-2.90826	0.76164	-3.818	0.000134
		Quadratic (P_2)	0.66249	0.69616	0.952	0.341286
		Cubic (P_3)	-0.78414	0.62363	-1.257	0.208616

In the absence of predators, egg and 1st instar mortality ranged between 1% and 15%, thus reflecting very little natural or manipulation mortality; therefore data for functional response did not have to be corrected.

Both predatory species displayed a type 2 functional response when fed on TPP eggs or 1st instar nymphs, as revealed by significant negative values of P_1 (Table 2).

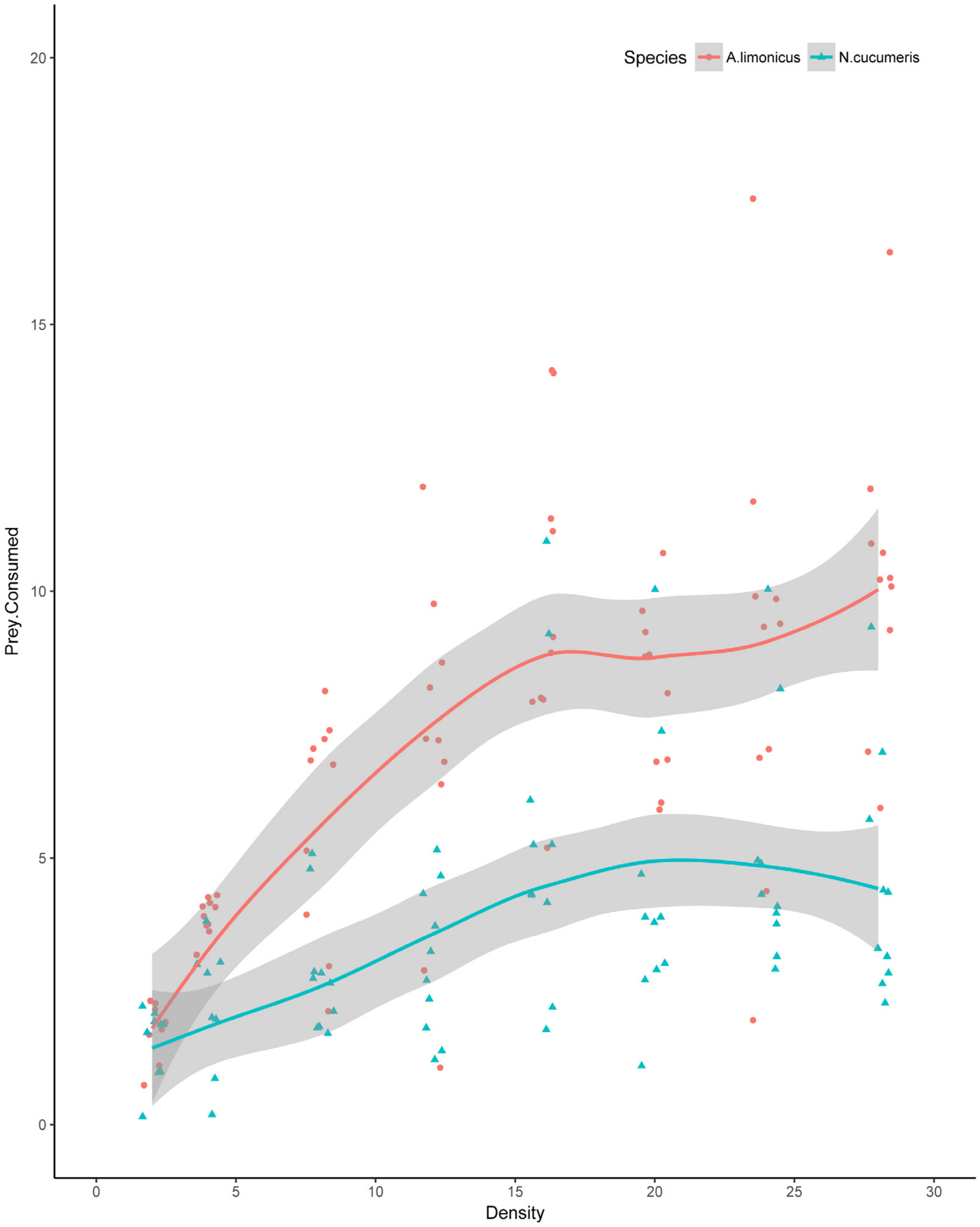

FIGURE 1. Functional response of adult female *A. limonicus* (upper line and round dots) and *N. cucumeris* (lower line and triangular dots) fed on TPP eggs. Points represent the observed number of prey consumed at each initial prey density. Grey areas around the curves represent 95% confidence intervals.

Handling time and attack rate

Amblydromalus limonicus had a higher attack rate than *N. cucumeris* for both eggs (>1.6 times) and 1st instar nymphs (3 times) (Table 3). However, *N. cucumeris* had a longer handling time than *A. limonicus* for both eggs (>twice) and 1st instar nymphs (>twice) (Table 3).

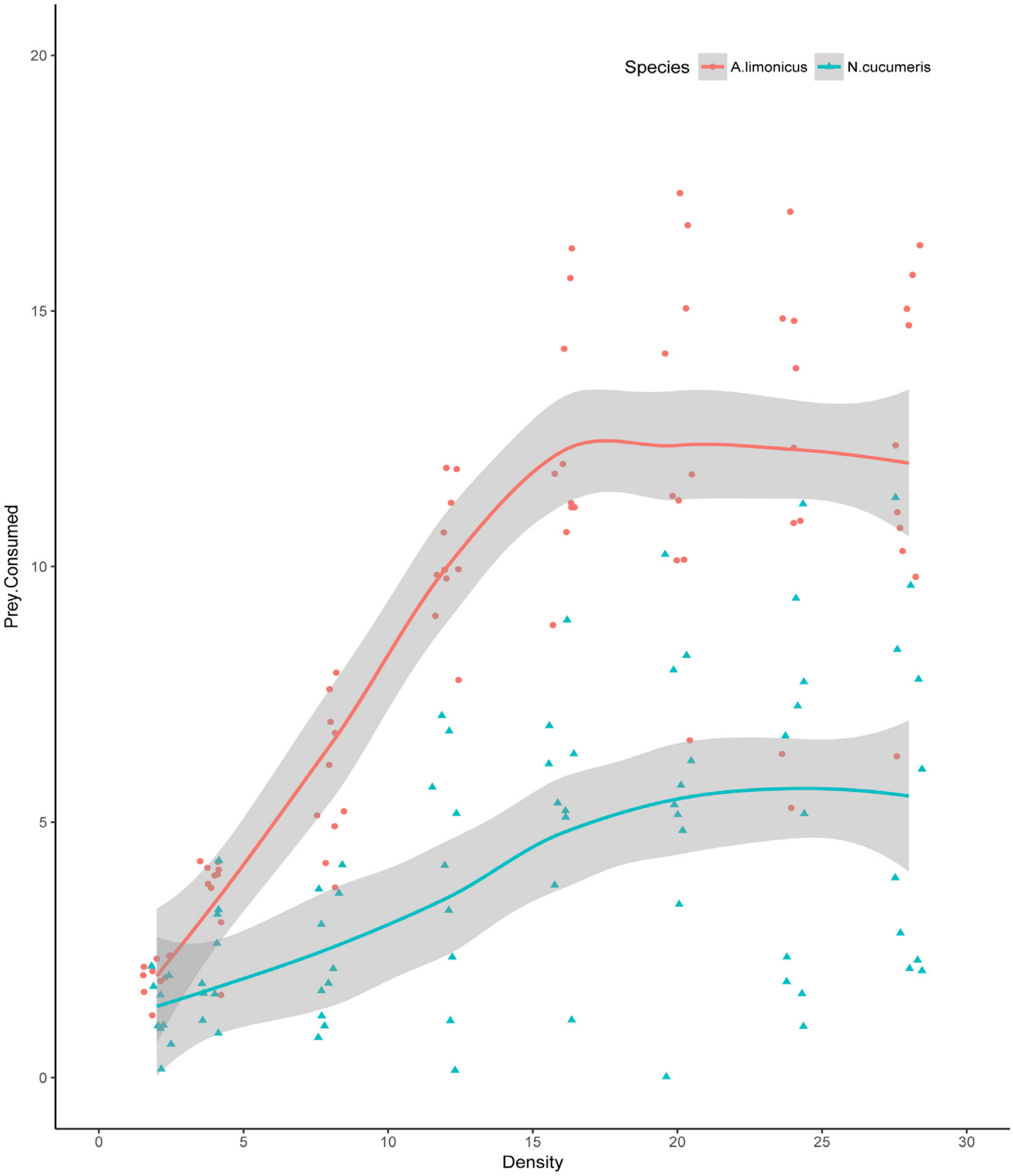

FIGURE 2. Functional response of adult female *A. limonicus* (upper line and round dots) and *N. cucumeris* (lower line and triangular dots) fed on TPP 1st instar nymphs. Points represent the observed number of prey consumed at each initial prey density. Grey areas around the curves represent 95% confidence intervals.

Reproductive rates

The interaction between predator species and density on an egg diet was not significant for the number of eggs laid (F=1.437; df=7; *P*=0.195). While density had no significant effect on the reproductive rate (F=1.543; df=7; *P*=0.157), predator species did have an effect on the number of eggs laid (F=29.569; df=1; *P*=0.000). *A. limonicus* had a much higher reproductive rate than *N. cucumeris* across all densities when fed on eggs (Table 4).

The interaction between predator species and density when fed on 1st instar nymphs was significant for the number of eggs laid, indicating that the two species showed different responses to prey density (F=2.772; df=7; *P*=0.010; Table 4). There was no significant density effect on the reproductive rate (F=1.207; df=7; *P*=0.302); however, there was an effect of predator species on the number of eggs laid (F=87.309; df=1; *P*=0.000). *A. limonicus* had a significantly higher reproductive rate than *N. cucumeris* across all densities when fed on 1st instar nymphs (Table 4).

TABLE 3. Mean values ± SE of attack rate and handling time (hours) for *A. limonicus* and *N. cucumeris* feeding on different life stages of TPP.

Predator Species	Prey Stage	Attack Rate (Asymptotic 95% CI)	Handling time (T_h) (Asymptotic 95% CI)
A. limonicus	Egg	0.05 ± 0.01 (0.03–0.07)	1.74 ± 0.23 (1.28–2.20)
	1st Instar nymph	0.06 ± 0.01 (0.04–0.08)	1.15 ± 0.15 (0.85–1.45)
N. cucumeris	Egg	0.03 ± 0.01 (0.01–0.05)	3.68 ± 0.67 (2.37–5.00)
	1st Instar nymph	0.02 ± 0.01 (0.01–0.03)	2.50 ± 0.79 (0.96–4.40)

TABLE 4. The number of eggs laid by *A. limonicus* and *N. cucumeris* at each density when fed on an diet of TPP eggs or 1st instar nymphs. Data are presented in the format of mean ± s.e. The number of replicates is 10 for each density.

Prey density	*A. limonicus*		*N. cucumeris*	
	Eggs of TPP	1st instar nymphs of TPP	Eggs of TPP	1st instar nymphs of TPP
2	0.80 ± 0.29	0.70 ± 0.30	0.40 ± 0.16	0.20 ± 0.13
4	1.80 ± 0.25	1.80 ± 0.36	0.60 ± 0.22	0.00 ± 0.00
8	1.60 ± 0.45	1.90 ± 0.43	0.70 ± 0.21	0.10 ± 0.10
12	1.70 ± 0.42	1.50 ± 0.40	0.50 ± 0.17	0.00± 0.00
16	2.10 ± 0.23	0.90 ± 0.28	0.60 ± 0.22	0.00 ± 0.00
20	1.20 ± 0.33	1.50 ± 0.40	0.80 ± 0.25	0.20 ± 0.13
24	1.10 ± 0.28	1.60 ± 0.31	0.80 ± 0.25	0.00 ± 0.00
28	1.00 ± 0.39	0.80 ± 0.25	0.60 ± 0.27	0.60 ± 0.22

Discussion

In this study, we compared the functional responses of *A. limonicus* and *N. cucumeris* to the density of TPP eggs or 1st instar nymphs. The negative values estimated for the linear parameters as well as the inverse density-dependant relationship between the proportion of prey consumed and initial prey density of eggs and 1st star nymphs indicate a type 2 functional response for both *A. limonicus* and *N. cucumeris*. In several phytoseiid species, type 2 functional response is common, including *N. cucumeris* on western flower thrips (Shipp & Whitfield 1991), *N. cucumeris*, *Neoseiulus barkeri*, and *Euseius nicholsi* on *Thrips flavidulus* (Yao *et al.* 2014), *N. cucumeris* on *Thrips tabaci* larvae (Madadi *et al*. 2007), and *N. cucumeris* on *T. tabaci* (Nielsen *et al.* 2014). Predators with a type 2 functional response have proved to be efficient, especially at low prey densities (Koehler 1999). Patel & Zhang (2017) estimated the predation rates of TPP eggs and 1st instar nymphs by *A.*

limonicus and *N. cucumeris* at the fixed density of 10 and the results are in line with our results in this paper. For example, *A. limonicus* consumed on average 6.17 eggs when offered 10 TPP eggs in Patel & Zhang (2017), and in this study, *A. limonicus* consumed 5.70 TPP eggs when offered 8 and 7.00 TPP eggs when offered 12.

Predation rates for both species increased with increasing prey density, perhaps due to interference or disturbance by the prey. This has been noticed in *Amblyseius largoensis*, *Euseius corcordis*, and *Galendromus (=Typhlodromus) helveolus* (Sandness & McMurtry 1970). At higher prey densities, the amount of time spent on consuming individual prey may be reduced because prey may accidently bump into a feeding predator, which could cause the predator to abandon the prey it is eating and attack another prey. The bumping of prey into each other (only for first instar nymphs of TPP here) could cause the prey to move, therefore increasing its chances of encountering a predator. This higher prey density causes wasteful killing (Metz *et al*. 1988) as a predator may partially consume the prey instead of eating one whole prey.

Even though it is common to have a type 2 functional response among phytoseiid species, functional responses may change due to a number of factors. In our study, *N. cucumeris* displayed a type 2 functional response when fed on TPP eggs and 1st instar nymphs; however, when Fang *et al.* (2013) compared the effectiveness of *N. cucumeris* and *N. barkeri* in controlling the citrus psyllid (*Diaphorina citri*) in China, the functional response of *N. cucumeris* was type 3 when fed *D. citri* eggs. Reaction to environmental conditions may cause a type 2 response shifting to a type 3 response. Functional response may be influenced by different factors, e.g. abiotic, such as temperature and relative humidity, and biotic, such as prey or host species (Donnelly & Phillips 2001; Hoddle 2003; Allahyari *et al.* 2004; Faria *et al*. 2004); the presence of alternative food (Wei & Walde 1997); predator sex (Parajulee *et al.* 1994) and predator age and feeding history (Eveleigh & Chant 1981). In addition, the host plant may also influence functional response, for instance indirectly, by affecting prey palatability or offering prey refuges (Messina & Hanks 1998) or directly, by plant structure such as trichome or by sticky exudates that reduce searching efficiency (Cedola *et al.* 2001). Holling (1965) stated that predators that have a type 3 functional response contribute to regulating their prey populations because this type of response allows for long-term persistence.

Attack rate and handling time are parameters that also help determine the magnitude of functional responses (Omkar 2005). The handling time is an important and reliable indicator of the amount of prey consumed and the predator efficiency as it determines the cumulative time spent on capturing, killing, and digesting the prey (Veeravel & Baskaran 1997). *A. limonicus* had an attack rate of 0.05 for eggs and 0.06 for 1st instar nymphs, whereas *N. cucumeris* had an attack rate of 0.03 for eggs and 0.02 for 1st instar nymphs. The attack rates of two prey stages were similar within each predator species, which could be due to the TPP eggs and 1st instar nymphs being similar in size. However, there was a significant difference between predator species: *A. limonicus* had a higher attack rate for both prey stages of TPP than *N. cucumeris* had. This implies *A. limonicus* could be a more effective control agent in early infestation when the prey population is comprised of more TPP eggs and 1st instar nymphal stage.

Furthermore, *A. limonicus* had a handling time of 1.74 hrs for eggs and 1.15 hrs for 1st instar nymphs, whereas *N. cucumeris* had a handling time of 3.68 hrs for eggs and 2.50 hrs for 1st instar nymphs. For both species of predatory mites, handling time for eggs was higher than for 1st instar nymphs. Various factors may affect handling time such as predator speed, movement of prey, and the time spent subduing individual prey (Hassell 1978), which could possibly be related to behavioural and physical prey attributes (Ali *et al.* 2011). Madadi *et al.* (2007) and Yao *et al.* (2014) also demonstrated similar results to our study in regards to attack rate and handling time as both studies investigated the functional response of *N. cucumeris* on *Thrips tabaci* larvae and first instar of *T. flavidulus*. Madadi *et al.* (2007) indicated the attack rate for *N. cucumeris* was 0.048 and the handling time was 1.030 hrs at 25°C. Yao *et al.* (2014) indicated the attack rate for *N. cucumeris* was 0.8856 and the handling time was 0.0298 hrs at 26°C. Making direct comparisons of these estimates by these authors with our results is, however, problematic due to differences in prey, environmental conditions, and prior predator adaptation to the tested prey.

Unlike the functional response, the numerical response of both species did not increase with prey density. There was no apparent trend of reproductive rates across densities for both TPP eggs and 1st instar nymphs. However, *A. limonicus* consistently produced significantly more eggs than did *N. cucumeris* across all densities when fed on an diet of either eggs or 1st instar nymph of TPP. The implications of a non-significant numerical response are that both predatory mite species would be unable to keep up with the growth of a TPP population if infestation should occur. Therefore, as suggested previously by Xu & Zhang (2015), inoculative releases would be required to prevent pest development in the early season; this may be achieved by the release of biocontrol agents to allow reproduction on alternative food such as pollen to occur before prey build-up. This would enable the setting up of a longer term control by keeping TPP populations to low levels—prevention rather than a curative control.

Nevertheless, functional response experiments carried out under laboratory conditions may have limited value for determining characteristics of predation in a natural setting. Some of the criticisms are that: the small arenas used to carry out the experiments may not be representative of the natural searching ability of a predator; environmental complexity cannot be easily replicated through a simple experimental arena; and plant characteristics can also affect predation response of a predator (Messina & Hanks 1998; O'Neil 1989). Great caution is therefore needed in extrapolating the results of oversimplified laboratory experiments to more complex and heterogeneous field conditions. Future experiments, being carried out on greenhouse potted plants to show more realistic predator-prey interaction, will be reported in a future paper.

Acknowledgements

The senior author would like to thank her parents and family for their unconditional encouragement and inspiration to her over the course of her education. She would also like to thank The University of Auckland for financial support and Landcare Research, Auckland, for supporting and providing her with the facilities she needed for her thesis. We thank Mr Chris Winks (Landcare Research, Auckland) for assistance and technical support in the laboratory, and Mr Kevin Chang and Dr Andrew Paul Balemi (The University of Auckland, Auckland) for help with statistical analyses. We also express our gratitude to Ms Anne Austin (Landcare Research, Lincoln), Miss Guangyun Li, Mr Jianfeng Liu, and Miss Melissa Kirk (The University of Auckland, Tamaki Campus) for their help and comments on the manuscript. The junior author was supported in part by "Core Funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science and Innovation Group" for his research on New Zealand mites.

References

Ali, M.P., Naif, A.A. & Huang, D. (2011) Prey consumption and functional response of a phytoseiid predator, *Neoseiulus womersleyi*, feeding on spider mite, *Tetranychus macfarlanei*. *Journal of Insect Science*, 11, 167.
https://doi.org/10.1093/jis/11.1.167

Allahyari, H., Fard, P.A. & Nozari, J. (2004) Effects of host on functional response of offspring in two populations of *Trissolcus grandis* on the sunn pest. *Journal of Applied Entomology*, 128, 39–43.

https://doi.org/10.1046/j.1439-0418.2003.00804.x

Arthurs, S., McKenzie, C.L., Chen, J., Dogramaci, M., Brennan, M., Houben, K. & Osborne, L. (2009) Evaluation of *Neoseiulus cucumeris* and *Amblyseius swirskii* (Acari: Phytoseiidae) as biological control agents of chilli thrips, *Scirtothrips dorsalis* (Thysanoptera: Thripidae) on pepper. *Biological Control*, 49, 91–96. https://doi.org/10.1016/j.biocontrol.2009.01.002

Butler, C.D. & Trumble, J.T. (2012) The potato psyllid, *Bactericera cockerelli* (Sulc)(Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies. *Terrestrial Arthropod Reviews*, 5, 87–111. https://doi.org/10.1163/187498312X634266

Cédola, C.V., Sánchez, N.E. & Liljesthröm, G.G. (2001) Effect of tomato leaf hairiness on functional and numerical response of *Neoseiulus californicus* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 25, 819–831. https://doi.org/10.1023/A:1020499624661

Chorąży, A., Kropczyńska-Linkiewicz, D., Sas, D. & Escudero-Colomar, L.A. (2016) Distribution of *Amblydromalus limonicus* in northeastern Spain and diversity of phytoseiid mites (Acari: phytoseiidae) in tomato and other vegetable crops after its introduction. *Experimental and Applied Acarology*, 69, 465–478. https://doi.org/10.1007/s10493-016-0050-5

Donnelly, B.E. & Phillips, T.W. (2001) Functional response of *Xylocoris flavipes* (Hemiptera: Anthocoridae) effects of prey species and habitat. *Environmental Entomology*, 30, 617–624. https://doi.org/10.1603/0046-225X-30.3.617

Eveleigh, E.S. & Chant, D.A. (1981) Experimental studies on acarine predator–prey interactions: effects of predator age and feeding history on prey consumption and the functional response (Acarina: Phytoseiidae). *Canadian Journal of Zoology*, 59, 1387–1406. https://doi.org/10.1139/z81-191

Fang, X., Lu, H., Ouyang, G., Xia, Y., Guo, M. & Wu, W. (2013) Effectiveness of two predatory mite species (Acari: Phytoseiidae) in controlling *Diaphorina citri* (Hemiptera: Liviidae). *Florida Entomologist*, 96, 1325–1333. https://doi.org/10.1653/024.096.0411

Faria, L.D.B., Godoy, W.A.C. & Trinca, L.A. (2004) Dynamics of handling time and functional response by larvae of *Chrysomya albiceps* (Dipt., Calliphoridae) on different prey species. *Journal of Applied Entomology*, 128, 432–436. https://doi.org/10.1111/j.1439-0418.2004.00868.x

Hassell, M.P. (1978) *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, NJ, 248 pp.

Hoddle, M.S. (2003) The effect of prey species and environmental complexity on the functional response of *Franklinothrips orizabensis*: a test of the fractal foraging model. *Ecological Entomology*, 28, 309–318. https://doi.org/10.1046/j.1365-2311.2003.00518.x

Holling, C.S. (1959a) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, 91, 293–320. https://doi.org/10.4039/Ent91293-5

Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91, 385–398. https://doi.org/10.4039/Ent91385-7

Holling, C.S. (1961) Principles of insect predation. *Annual Review of Entomology*, 6, 163–182. https://doi.org/10.1146/annurev.en.06.010161.001115

Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, 97, 5–60. https://doi.org/10.4039/entm9745fv

Juliano, S.A. (2001) Nonlinear curve fitting: predation and functional response curves. *Design and Analysis of Ecological Experiments*, 2, 178–196.

Juan-Blasco, M., Qureshi, J.A., Urbaneja, A. & Stansly, P.A. (2012) Predatory mite, *Amblyseius swirskii* (Acari: Phytoseiidae), for biological control of Asian citrus psyllid, *Diaphorina citri* (Hemiptera: Psyllidae). *Florida Entomologist*, 95, 543–551. https://doi.org/10.1653/024.095.0302

Kar, F., Lin, S. & Zhang, Z.Q. (2015) *Neocypholaelaps novaehollandiae* Evans (Acari: Ameroseiidae) rediscovered: experiments on its life history and behaviour. *New Zealand Entomologist*, 38, 126–133. https://doi.org/10.1080/00779962.2015.1043043

Knapp, M., van Houten, Y., Hoogerbrugge, H. & Bolckmans, K. (2013) *Amblydromalus limonicus* (Acari: Phytoseiidae) as a biocontrol agent: literature review and new findings. *Acarologia*, 53, 191–202. https://doi.org/10.1051/acarologia/20132088

Koehler, H.H. (1999) Predatory mites (Gamasina, Mesostigmata). *Agriculture, Ecosystems & Environment*, 74, 395–410. https://doi.org/10.1016/S0167-8809(99)00045-6

Kratina, P., Vos, M., Bateman, A. & Anholt, B.R. (2009) Functional responses modified by predator density. *Oecologia*, 159, 425–433. https://doi.org/10.1007/s00442-008-1225-5

Liu, J.F. & Zhang Z.Q. (2017) Development, survival and reproduction of a New Zealand strain of *Amblydromalus limonicus* (Acari: Phytoseiidae) on *Typha orientalis* pollen, *Ephestia kuehniella* eggs, and an artificial diet. *International Journal of Acarology,* 43, 153–159. https://doi.org/10.1080/01647954.2016.1273972

Madadi, H., Enkegaard, A., Brodsgaard, H.F., Kharrazi-Pakdel, A., Mohaghegh, J. & Ashouri, A. (2007) Host plant effects on the functional response of *Neoseiulus cucumeris* to onion thrips larvae. *Journal of Applied Entomology,* 131, 728–733. https://doi.org/10.1111/j.1439-0418.2007.01206.x

Mauchline, N.A., Stannard, K.A. & Zydenbos, S.M. (2013) Evaluation of selected entomopathogenic fungi and bio-insecticides against *Bactericera cockerelli* (Hemiptera). *New Zealand Plant Protection*, 66, 324–332.

McMurtry, J.A., De Moraes, G.J. & Sourassou, N.F. (2013) Revision of the lifestyles of phytoseiid mites (Acari: Phytoseiidae) and implications for biological control strategies. *Systematic and Applied Acarology*, 18, 297–320. https://doi.org/10.11158/saa.18.4.1

McMurtry, J.A. & Scriven, G.T. (1971) Predation by *Amblyseius limonicus* on *Oligonychus punicae* (Acarina): Effects of initial predator-prey ratios and prey distribution. *Annals of the Entomological Society of America*, 64, 219–224. https://doi.org/10.1093/aesa/64.1.219

Medd, N.C. & GreatRex, R.M. (2014) An evaluation of three predatory mite species for the control of greenhouse whitefly (*Trialeurodes vaporariorum*). *Pest Management Science*, 70, 1492–1496. https://doi.org/10.1002/ps.3794

Messelink, G.J., Van Steenpaal, S.E. & Ramakers, P.M. (2006) Evaluation of phytoseiid predators for control of western flower thrips on greenhouse cucumber. *BioControl*, 51, 753–768. https://doi.org/10.1007/s10526-006-9013-9

Messina, F.J. & Hanks, J.B. (1998) Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environmental Entomology*, 27, 1196–1202. https://doi.org/10.1093/ee/27.5.1196

Metz, J.A., Sabelis, M.W. & Kuchlein, J.H. (1988) Sources of variation in predation rates at high prey densities: an analytic model and a mite example. *Experimental and Applied Acarology*, 5, 187–205. https://doi.org/10.1007/BF02366094

Nielsen, M.C., Davidson, M.M. & Butler, R.C. (2014) Predation rate of Thrips tabaci larvae by *Neoseiulus cucumeris* is influenced by prey density and presence of a host plant. *New Zealand Plant Protection,* 67, 197–203.

O'Neil, R.J. (1989) Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). *Journal of the Kansas Entomological Society*, 148–155.

Opit, G.P., Nechols, J.R. & Margolies, D.C. (2004) Biological control of twospotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae), using *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseidae) on ivy geranium: assessment of predator release ratios. *Biological Control,* 29, 445–452. https://doi.org/10.1016/j.biocontrol.2003.08.007

Parajulee, M.N., Phillips, T.W. & Hogg, D.B. (1994) Functional response of *Lyctocoris campestris* (F.) adults: effects of predator sex, prey species, and experimental habitat. *Biological Control*, 4, 80–87. https://doi.org/10.1006/bcon.1994.1014

Patel, K. & Zhang, Z.Q. (2017) Prey preference and reproduction of predatory mites, *Amblybromalus limonicus* and *Neoseiulus cucumeris,* on eggs of and 1st instar nymphs of the Tomato/Potato Psyllid. *Interna-*

tional Journal of Acarology, 43(6), 468–474.
http://dx.doi.org/10.1080/01647954.2017.1349177

Omkar, P.A. (2005) Functional responses of coccinellid predators: an illustration of a logistic approach. *Journal of Insect Science*, 5, 1–6.
https://doi.org/10.1673/031.005.0501

Rahman, V.J., Babu, A., Roobakkumar, A. & Perumalsamy, K. (2012) Functional and numerical responses of the predatory mite, *Neoseiulus longispinosus,* to the red spider mite, *Oligonychus coffeae,* infesting tea. *Journal of Insect Science*, 12, 125.
https://doi.org/10.1673/031.012.12501

Sandness, J.N. & McMurtry, J.A. (1970) Functional response of three species of Phytoseiidae (Acarina) to prey density. *The Canadian Entomologist*, 102, 692–704.
https://doi.org/10.4039/Ent102692-6

Sepúlveda, F. & Carrillo, R. (2008) Functional response of the predatory mite *Chileseius camposi* (Acarina: Phytoseiidae) on densities of its prey, *Panonychus ulmi* (Acarina: Tetranychidae). *Revista de Biología Tropical*, 56, 1255–1260.

Shipp, J.L. & Whitfield, G.H. (1991) Functional response of the predatory mite, *Amblyseius cucumeris* (Acari: Phytoseiidae), on western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae). *Environmental Entomology*, 20, 694–699.
https://doi.org/10.1093/ee/20.2.694

Solomon, M.E. (1949) The natural control of animal populations. *The Journal of Animal Ecology*, 18(1), 1–35.
https://doi.org/10.2307/1578

Van Lenteren, J.C. (2012) The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. *BioControl*, 57, 1−20.
https://doi.org/10.1007/s10526-011-9395-1

Veeravel, R. & Baskaran, P. (1997) Functional and numerical Responses of *Coccinella transversalis* Fab. and *Cheilomenes sexmaculatus* Fab. feeding on the Melon Aphid, *Aphis gossypii* Glov. *International Journal of Tropical Insect Science*, 17, 335–339.
https://doi.org/10.1017/S1742758400019159

Walker, G.P., MacDonald, F.H., Wright, P.J., Puketapu, A.J., Gardner-Gee, R., Connolly, P.G. & Anderson, J.A. (2015) Development of Action Thresholds for Management of *Bactericera cockerelli* and Zebra Chip Disease in Potatoes at Pukekohe, New Zealand. *American Journal of Potato Research*, 92, 266–275.
https://doi.org/10.1007/s12230-014-9427-3

Wei, Q. & Walde, S.J. (1997) The functional response of *Typhlodromus pyri* to its prey, *Panonychus ulmi*: the effect of pollen. *Experimental and Applied Acarology*, 21, 677–684.
https://doi.org/10.1007/BF02803510

Xu, Y. & Zhang, Z.Q. (2015) *Amblydromalus limonicus*: a “new association” predatory mite against an invasive psyllid (*Bactericera cockerelli*) in New Zealand. *Systematic and Applied Acarology*, 20, 375–382.
https://doi.org/10.11158/saa.20.4.3

Yao, H., Zheng, W., Tariq, K. & Zhang, H. (2014) Functional and numerical responses of three species of predatory phytoseiid mites (Acari: Phytoseiidae) to *Thrips flavidulus* (Thysanoptera: Thripidae). *Neotropical Entomology*, 43, 437–445.
https://doi.org/10.1007/s13744-014-0229-6

Submitted: 28 Jun. 2017; accepted by Qing-Hai Fan: 3 Aug. 2017; published: 1 Sept. 2017