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Cost-effective and efficient factitious prey for mass production of *Neoseiulus cucumeris* (Acari: Phytoseiidae): assessing its quality compared with natural prey

Shima Yazdanpanah¹, Yaghub Fathipour^{1*} , Elham Riahi¹ and Myron P. Zalucki²

Abstract

Background: Using alternative diets for the mass production of phytoseiid predatory mites may facilitate their cost-effective rearing. Factitious prey is often used as an alternative food source for mass rearing of generalist phytoseiids. The generalist predator, *Neoseiulus cucumeris* (Oudemans), is a commercially available biocontrol agent against various pests. We assessed the suitability of two factitious prey, *Ephestia kuehniella* Zeller eggs and *Tyrophagus putrescentiae* (Schrank), as diets for long-term rearing (up to 30 generations) of *N. cucumeris*, when compared with a natural prey, *Tetranychus urticae* Koch.

Results: The predator completed its development on all tested diets successfully. Under laboratory conditions, *Tyrophagus putrescentiae* could support the development and oviposition of the predator for up to 30 generations even better than its natural prey *T. urticae*. However, the eggs of *E. kuehniella* were not suitable for this predator because of the longer pre-adult period and adults failed to reproduce.

Conclusions: Since rearing on *T. putrescentiae* for a long time had no adverse effects on the predator's performance, this factitious prey could be considered as a suitable and cost-effective diet for mass production of *N. cucumeris*.

Keywords: Mass rearing, *Neoseiulus cucumeris*, *Tyrophagus putrescentiae*, *Tetranychus urticae*, *Ephestia kuehniella*, Predation capacity

Background

The two-spotted spider mite, *Tetranychus urticae* Koch, is one of the major pests of agricultural crops grown worldwide and is found on approximately 1200 host plant species in 70 genera (Do Amaral et al. 2020). Management of *T. urticae* is difficult and pesticides are often used for this purpose. The ability of *T. urticae* to develop resistance to a range of chemicals has created critical situations for practical pest control. To overcome this problem a more durable crop protection solution based on

integrated pest management (IPM) systems is necessary (Sedaratian et al. 2009).

Phytoseiid mites play a major role in keeping phytophagous mite populations at low densities and decreasing their deleterious impact (Al-Azzazy and Alhewairini 2020). Their high consumption rate of prey individuals, high reproductive rate, and rapid developmental rate make them important biological control agents (Hoy 2011). Flexibility in feeding behavior, such as feeding on alternative prey or feeding on non-prey foods, including fungal spores, nectar, and pollen has generally been observed in generalist phytoseiid species (Overmeer 1985). Most generalist phytoseiid mites use alternative food sources, promoting their persistence in the field

*Correspondence: fathi@modares.ac.ir

¹ Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P. O. Box 14115-336, Tehran, Iran
Full list of author information is available at the end of the article

when prey is absent or scarce, and facilitating their mass-rearing for augmentative biological control purposes (McMurtry et al. 2013; Yazdanpanah et al. 2021).

Neoseiulus cucumeris (Oudemans), a generalist predatory phytoseiid mite, is known to feed on the immature stages of various pests. The broad prey range and ability to survive on plant pollen categorized it as a type III lifestyle (subtype III-e) predator (McMurtry et al. 2013). Mass rearing aims to cost-effectively produce a large number of efficient predators in a short time available commercially for augmentative release (Nordlund 1998). Cost-effective rearing of *N. cucumeris* on more economic food sources such as factitious prey would accelerate the mass production of this predator.

Generalist predatory mites can feed and develop on many different non-prey foods, including eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Calvo et al. 2015), and the stored product mite, *Tyrophagus putrescentiae* (Schrank) (Astigmatidae), which has been commonly used as a factitious prey for the commercial production of different phytoseiids, including *N. cucumeris* (Britto et al. 2012; Pirayeshfar et al. 2020).

The effects of long-term rearing and feeding on an alternative diet on a predator's performance need to be evaluated if such a diet is to be used for mass rearing (Bellutti 2011; Sørensen et al. 2012). In the present study, the predation capacity and life table parameters of *N. cucumeris* were determined after long-term feeding on *T. urticae* as one of its natural prey for the first time. In addition, we assessed the effects of long-time rearing of the predator on *T. putrescentiae*, and eggs of *E. kuehniella* as alternative prey, and then compared the population growth parameters and potential of this predator when reared long-term on its main prey and alternative foods.

Methods

Stock culture of two-spotted spider mite, *T. urticae*

An initial population of *T. urticae* was obtained from weeds growing around the Faculty of Agriculture, Tarbiat Modares University, Tehran, Iran. Some female and male specimens of the spider mite were mounted in Hoyer's medium on microscope slides and identified using the identification keys. The colony of *T. urticae* was established by releasing them onto cultivated beans (*Phaseolus vulgaris* L.) at the five-leaf stage. New bean plants were planted and added to the colony weekly. The *T. urticae* colony was kept under greenhouse conditions.

Eggs of the Mediterranean flour moth, *E. kuehniella*

Eggs of *E. kuehniella* were obtained from a colony that had been established at the laboratory of the Faculty of

Agriculture, Tarbiat Modares University, Tehran, Iran. Before the experiments.

Fresh eggs (less than 24 h old) were kept in a freezer (-18°C for 48 h) and refrigerated (4°C) for up to two weeks.

Stock culture of stored product mite, *T. putrescentiae*

The individuals of *T. putrescentiae* were originally collected from infested Petri dishes containing the fungus *Alternaria* sp., and then reared on wheat bran at $27 \pm 1^{\circ}\text{C}$, $60\% \pm 5$ RH, and a photoperiod of 16L:8D h in a Plexiglas container ($10 \times 7 \times 4$ cm).

Stock culture of the phytoseiid predator, *N. cucumeris*

The stock culture of *N. cucumeris* was obtained from Bio-Planet, Italy. Individuals were transferred to a green plastic sheet ($16 \times 11 \times 0.1$ cm) sitting atop a water-soaked sponge in a Plexiglas container ($30 \times 15 \times 12$ cm). All edges of the plastic sheet were covered by moist tissue paper which prevented mites from escaping (Walzer and Schausberger 1999). Water was put in the containers daily to prevent the strips from drying out. Some cotton fibers were added to the plastic sheet to provide a substrate for oviposition. The stock cultures of *N. cucumeris* were kept in a growth chamber at $25 \pm 1^{\circ}\text{C}$, $60 \pm 5\%$ RH, and a photoperiod of 16L:8D h. A mixture of pre-adult stages of *T. urticae* (about 1000–2000) for the rearing of *N. cucumeris* on *T. urticae* and a mixture of immature stages of *T. putrescentiae* (2000–3000) for rearing this predator on *T. putrescentiae* was offered as food two times a week.

Experimental setup

The experimental units were quite similar to the stock culture rearing units but smaller. The 3-cm-diameter units consisted of green plastic sheets ($3 \times 3 \times 0.1$ cm), plastic trays ($7 \times 5 \times 4$ cm), and wet sponges. About 40 pairs of *N. cucumeris* were selected randomly from the stock culture and kept in a new experimental unit for less than 24 h so as to have the same-aged eggs as the predator. The newly laid eggs were transferred to the experimental units individually. After larval emergence, one of the three diets (*T. putrescentiae*, *T. urticae*, and eggs of *E. kuehniella*) was offered. For the experiments, about 30–40 and 50–60 nymphs of *T. urticae* were provided daily for the nymphs and adults of the predator, respectively. About 3–5 eggs of *E. kuehniella* were offered to the experimental units as a diet every day, and about 50–70 pre-adult stages of *T. putrescentiae* were used at two-day intervals. After adult emergence, females were coupled with the males of the same treatment. All replicates of each treatment were monitored daily to record development, fecundity, longevity, and survival rate. Since most

N. cucumeris immatures could not complete their development and reach adulthood on the eggs of *E. kuehniella* this diet treatment was discontinued but the mentioned procedure was repeated for generations of 10, 20, and 30 of *N. cucumeris* colonies that were fed on *T. putrescentiae* and *T. urticae*. All experiments were carried out in the laboratory at standard conditions (25 ± 1 °C, $60 \pm 5\%$ RH, and a photoperiod of 16L:8D h).

The predation capacity of *N. cucumeris* was determined on *T. urticae* as prey for predators maintained on *T. urticae* for 30 generations. First, an experiment was done to estimate the predation rate by adults of each sex. Same-aged mated adults (10 females and 10 males) were transferred singly to the experimental units (20 units total). About 50 immature *T. urticae* were allocated to each unit as food, and the number of mites consumed was recorded daily. The mean number of prey consumed was calculated for each sex. Finally, the ratio of the feeding rates of females to males was obtained per day to guide the main experiment. To calculate the predation rate of *N. cucumeris*, the number of consumed *T. urticae* was recorded daily during the life table experiments until the death of all individuals.

Data analysis

The two-sex life table procedure (Chi and Liu 1985; Chi 1988) using the TWSEX-MSChart software (Chi 2021) was used to calculate the life table parameters and analyze data of *N. cucumeris* at different generations on each diet tested. The variances and standard errors of all parameters, including the gross reproductive rate (GRR), net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T) were estimated using the bootstrap procedure with 100,000 samples. Multiple comparisons for different generations as well as diets were carried out using the paired bootstrap test in TWSEX-MSChart software.

According to Chi and Yang (2003), the parameters of net predation rate (C_0) (mean number of *T. urticae* consumed by an individual predator during its life span), transformation rate (Q_p) (the number of *T. urticae* needed for the production of an offspring from a predator), stable predation rate (ψ) (the total predation capacity of a stable population), and finite predation rate (ω) (the predation potential of *N. cucumeris* population by combining its finite rate of increase [λ], age-stage predation rate [c_{xj}], and stable age-stage structure [a_{xj}]) were calculated using CONSUME-MSChart software (Chi 2021). The variances and standard errors of predation parameters were estimated using the bootstrap resampling method. The statistics of C_0 , Q_p , ψ , and ω were compared based on the paired bootstrap test (with 100,000 resampling), using the TWSEX-MS Chart program (Chi 2021).

Results

Life table parameters of *N. cucumeris* fed on *E. kuehniella*

The predator, *N. cucumeris*, did not feed consistently on the eggs of *E. kuehniella*, and about 7% of individuals reached adulthood. Only two females developed and lived less than 8 days without oviposition; therefore, no long-term rearing of *N. cucumeris* occurred on this diet. The mean duration of protonymph and deutonymph was 6.8 and 7.5 d, respectively. The age-stage-specific survival rates (s_{xj}) indicate the initiation and termination of all immature and adult life stages while survivorship (l_x) shows the probability that a newborn individual will survive to age x and is calculated by pooling all individuals of both sexes and clearly indicates the inadequacy of this diet (Fig. 1). Since a few individuals of *N. cucumeris* reached the adult stage and there was no fecundity, analyses of the life table data for this treatment were not possible.

Life table parameters of *N. cucumeris* fed on *T. putrescentiae*

Significant differences in the duration of immature stages were observed among different tested generations (Table 1). The larval period was the shortest immature stage in all generations tested. Both protonymphal and deutonymphal durations were longer in G1 compared with the other generations. The longest developmental time was in G1 (10.7 d). Female and male longevity

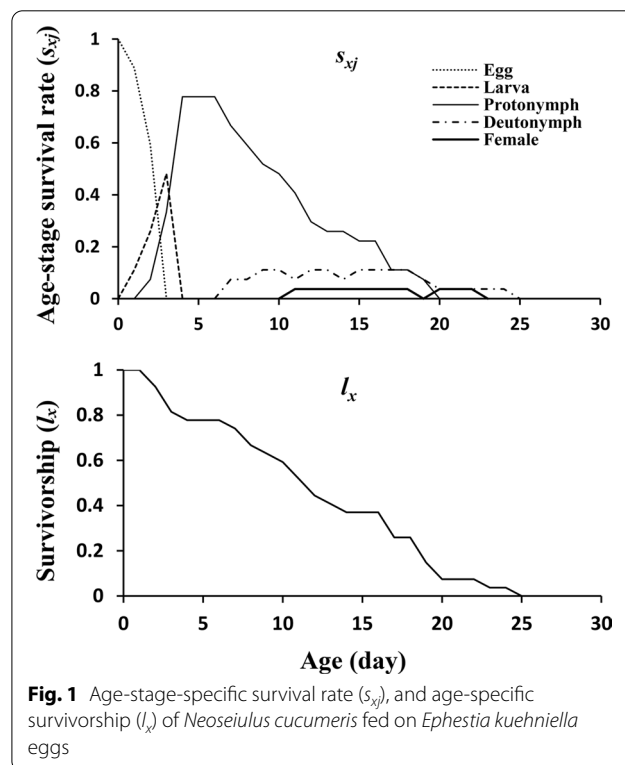


Fig. 1 Age-stage-specific survival rate (s_{xj}), and age-specific survivorship (l_x) of *Neoseiulus cucumeris* fed on *Ephestia kuehniella* eggs

Table 1 Long-term effects of feeding *Neoseiulus cucumeris* on *Tyrophagus putrescentiae*, *Tetranychus urticae*, and *Ephesthia kuehniella* on the duration of different life stages (days), fecundity (eggs/female) and immature survival (%) (Mean ± SE)

Parameter	<i>Tyrophagus putrescentiae</i>				<i>Tetranychus urticae</i>				<i>Ephesthia kuehniella</i>
	G1	G10	G20	G30	G1	G10	G20	G30	G1
Egg	2.26 ± 0.162 ^{abA}	1.77 ± 0.169 ^{ba}	2.52 ± 0.173 ^{abA}	2.26 ± 0.135 ^{abA}	2.41 ± 0.116 ^{abA}	2.09 ± 0.177 ^{abA}	2.38 ± 0.142 ^{abA}	2.29 ± 0.181 ^{abA}	2.43 ± 0.113
Larva	1.07 ± 0.072 ^{abA}	1.05 ± 0.044 ^{ba}	1.30 ± 0.096 ^{abA}	1.00 ± 0.000 ^{ba}	1.00 ± 0.00 ^{abA}	1.47 ± 0.462 ^{abA}	1.00 ± 0.00 ^{ab}	1.00 ± 0.00 ^{abA}	1.00 ± 0.000
Protonymph	2.92 ± 0.144 ^{abA}	2.09 ± 0.061 ^{ba}	2.00 ± 0.064 ^{abA}	2.00 ± 0.000 ^{ba}	2.10 ± 0.064 ^{ab}	2.32 ± 0.131 ^{abA}	1.83 ± 0.099 ^{ba}	2.06 ± 0.064 ^{abA}	6.80 ± 0.341
Deutonymph	4.43 ± 0.349 ^{abA}	1.86 ± 0.097 ^{ba}	1.90 ± 0.067 ^{ba}	1.92 ± 0.056 ^{ba}	1.7 ± 0.103 ^{bb}	2.16 ± 0.181 ^{abA}	1.86 ± 0.098 ^{abA}	1.75 ± 0.126 ^{abA}	7.50 ± 0.411
Pre-adult	10.71 ± 0.408 ^{abA}	6.77 ± 0.231 ^{cb}	7.70 ± 0.257 ^{ba}	7.13 ± 0.170 ^{bcA}	7.25 ± 0.157 ^{ab}	7.5 ± 0.240 ^{abA}	7.09 ± 0.191 ^{abA}	6.92 ± 0.187 ^{abA}	15.50 ± 1.317
Male longevity	38.12 ± 4.122 ^{abA}	33.65 ± 3.593 ^{abA}	18.33 ± 1.593 ^{bb}	35.19 ± 3.631 ^{abA}	22.5 ± 4.950 ^{ab}	25.6 ± 2.594 ^{abA}	26.33 ± 3.064 ^{abA}	30.83 ± 3.691 ^{abA}	–
Female longevity	61.19 ± 7.264 ^{abA}	52.15 ± 5.180 ^{abA}	36.41 ± 4.380 ^{abA}	48.44 ± 4.255 ^{abA}	28.68 ± 3.396 ^{ab}	25.0 ± 2.567 ^{ab}	25.23 ± 2.485 ^{ab}	25.33 ± 3.999 ^{ab}	5.50 ± 2.241
Total life span	54.62 ± 5.719 ^{abA}	44.58 ± 3.853 ^{abA}	31.92 ± 3.706 ^{ba}	42.38 ± 3.091 ^{abA}	27.45 ± 2.862 ^{ab}	25.17 ± 1.915 ^{ab}	25.68 ± 1.885 ^{abA}	28.08 ± 2.657 ^{ab}	21.00 ± 3.470
APOP	4.00 ± 0.288 ^{abA}	2.54 ± 0.141 ^{ba}	4.43 ± 0.961 ^{abA}	2.15 ± 0.102 ^{ca}	3.4 ± 0.424 ^{abA}	2.75 ± 0.446 ^{abA}	2.62 ± 0.208 ^{abA}	2.5 ± 0.219 ^{abA}	–
TPOP	14.60 ± 0.540 ^{abA}	9.85 ± 0.310 ^{bcA}	11.78 ± 1.038 ^{ba}	9.15 ± 0.268 ^{ca}	10.8 ± 0.506 ^{ab}	10.25 ± 0.637 ^{abA}	9.69 ± 0.171 ^{ab}	9.83 ± 0.393 ^{abA}	–
Oviposition period	19.53 ± 2.730 ^{abA}	24.00 ± 1.731 ^{abA}	13.58 ± 1.705 ^{ba}	24.69 ± 1.402 ^{abA}	15.2 ± 2.390 ^{abA}	9.75 ± 1.797 ^{ab}	12.08 ± 1.591 ^{abA}	13.5 ± 3.750 ^{abA}	–
Fecundity	27.27 ± 3.872 ^{ba}	44.69 ± 3.129 ^{abA}	18.27 ± 2.620 ^{ba}	47.91 ± 2.465 ^{abA}	27.56 ± 4.366 ^{abA}	9.92 ± 2.811 ^{bb}	22.76 ± 2.897 ^{abA}	24.67 ± 7.019 ^{ab}	–
Immature survival (%)	77 ± 0.080 ^{ba}	100 ± 0.000 ^{abA}	80 ± 0.008 ^{ba}	88 ± 0.060 ^{abA}	83 ± 0.076 ^{abA}	86 ± 0.076 ^{abA}	91 ± 0.056 ^{abA}	71 ± 0.110 ^{abA}	7.00 ± 0.301

G generation, APOP adult pre-oviposition period, TPOP total pre-oviposition period (from egg to first oviposition)

Means followed by different capital letters within the same row are comparisons between the corresponding generations of two diets. The means followed by different small letters within the same row are comparisons among different generations of each diet ($P < 0.05$, paired-bootstrap)

and the total lifespan (from birth to death) of *N. cucumeris* were not significantly different in G1, G10, and G30 (Table 1). The longest TPOP (total pre-oviposition period) was observed in G1. The oviposition period and fecundity of *N. cucumeris* in G10 and G30 were significantly higher than in the other tested generations (Table 1).

The adult stage started at 7, 5, 6, and 6 d in G1, G10, G20, and G30, respectively. Females of the first generation lived more days, while both sexes in G20 had the shortest lifetime (Fig. 2). Based on the fecundity curves, the highest daily fecundity was observed in G10 (2.69 eggs) at the age of 11 days, while the lowest was at the age of 12 days in G20 (1.5 eggs) (Fig. 3).

Analysis of life table parameters of *N. cucumeris* indicated differences among the tested generations (Table 2). There was no significant difference between generations in terms of *GRR*. The lowest value of R_0 was observed in G20, but was not significantly different compared with G1. The first generation had the lowest values of r and λ , as well as it had the longest T value (28.2 days) (Table 2).

Life table parameters of *N. cucumeris* fed on *T. urticae*

There were no significant differences in the duration of the egg, larva, total pre-adult, APOP, TPOP, female longevity, male longevity, total lifespan, oviposition, and immature survival (Table 1). G1, followed by G30 and

G20, had the highest value of fecundity (Table 1). The start of the adult stage differed little among the generations; 6, 6, 5, and 6 d in G1, G10, G20, and G30, respectively (Fig. 4). Females of the first generation lived longer (54 d) (Fig. 4). The life table parameters, including l_x , m_x , and f_{xj} of *N. cucumeris* during 30 generations of feeding on *T. urticae* (Fig. 5) indicated the highest fecundity was observed in G20 (2.25 eggs) at the age of 14 d. The analysis of the life table data of *N. cucumeris* showed significant differences among the tested generations (Table 2). Females in G1 had a higher *GRR* than the other generations. The parameters R_0 , r , and λ in G1 did not differ significantly from G20 and G30.

Life table parameters of *N. cucumeris* fed on *T. putrescentiae* versus *T. urticae*

In G1, the total development time of *N. cucumeris* was significantly shorter when the predator fed on *T. urticae* than on *T. putrescentiae*. The total lifespan of *N. cucumeris* was longer in G1, G10, and G30 when this predator fed on *T. putrescentiae*. The oviposition period and fecundity were significantly shorter in G10 when *T. urticae* was the food source. In addition, *GRR*, R_0 , r , and λ were substantially lower in G10 when feeding on *T. urticae* compared with feeding on *T. putrescentiae* in G10.

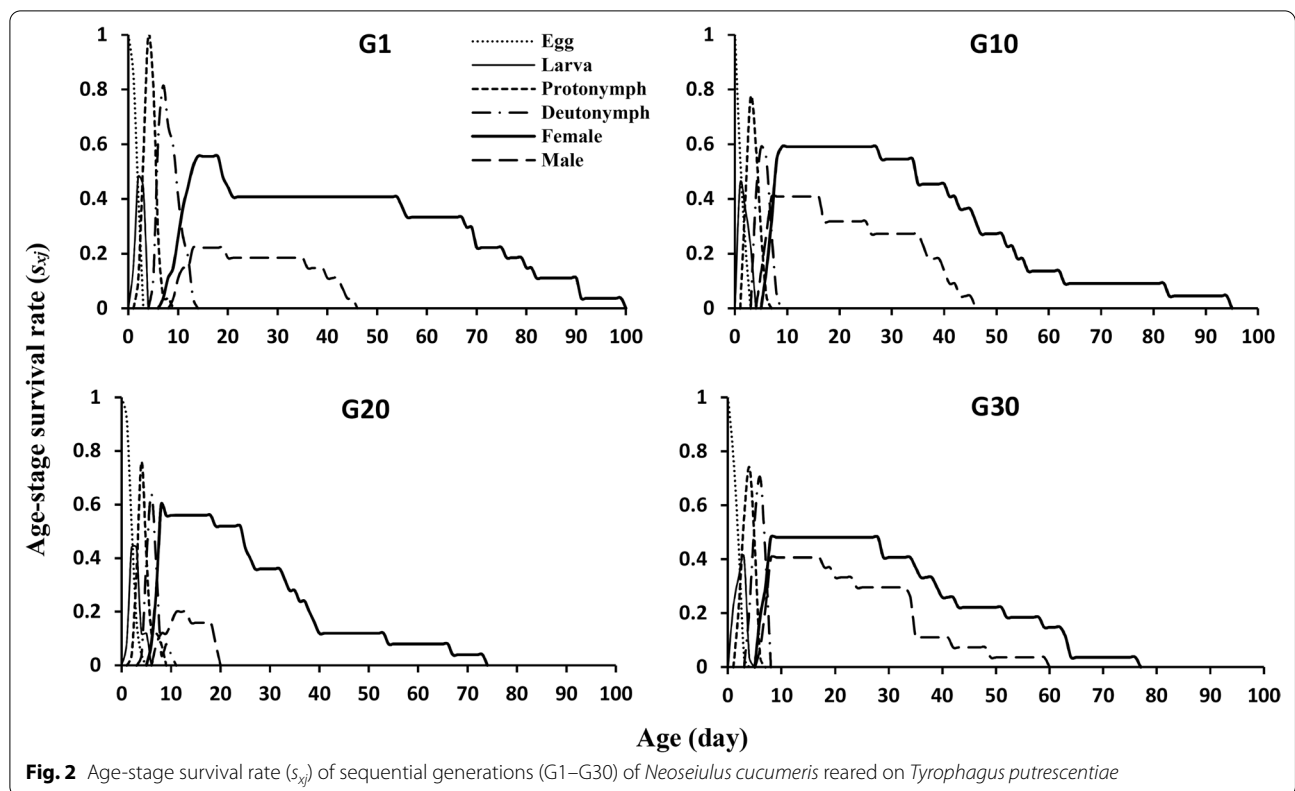


Fig. 2 Age-stage survival rate (s_{xy}) of sequential generations (G1–G30) of *Neoseiulus cucumeris* reared on *Tyrophagus putrescentiae*

Predation capacity of *N. cucumeris* after long-term feeding on *T. urticae*

No predation activity was observed by larvae in all treatments (Fig. 6). Age-stage-specific consumption rates increased with increasing predator stage; deutonymphs consumed more prey than protonymphs, and the same trend was observed for adults compared with deutonymphs. The predation rate of females during the oviposition period was higher than in pre- and post-oviposition periods (Fig. 6). The number of prey consumed by females was 36, 21, 18, and 21, whereas it was 22, 13, 11, and 11 for males in G1, G10, G20, and G30, respectively. The age-specific predation rate (k_x) is the mean number of *T. urticae* consumed by *N. cucumeris* at age x , and the age-specific net predation rate (q_x) can be determined by considering the survivorship (Fig. 7).

The highest value of the net predation rate (C_0) was 467 nymphs in G1, decreasing to 260, 166, and 238 prey in G10, G20, and G30, respectively (Table 3). According to the values of Q_p , *N. cucumeris* required a maximum of 49 prey (observed in G10) to produce an egg. The highest and lowest values of ψ and ω of *N. cucumeris* were observed in G1 and G20, respectively (Table 3).

Discussion

The effects of feeding on factitious and main prey on the performance of *N. cucumeris* have been studied but only after one generation (e.g., Sarwar 2009; Delisle et al. 2015; Li and Zhang 2016; Patel and Zhang 2017; Al-Shemmary 2018; Li et al. 2021) and long-term rearing on such diets on the effectiveness of *N. cucumeris* remains an open question. We evaluated the performance of *N. cucumeris* when offered either *T. urticae*, *T. putrescentiae*, or eggs of *E. kuehniella*. Furthermore, the predation capacity of this predator on nymphs of *T. urticae* was evaluated during long-term rearing.

Although *N. cucumeris* was able to successfully develop from egg to adult stage on all tested diets, feeding on the eggs of *E. kuehniella* led to high immature mortality. Whereas 83% and 77% of eggs reached adulthood when *T. urticae* and *T. putrescentiae* were offered as food, respectively, only 7% did so on *E. kuehniella*. We found that juvenile stages of *N. cucumeris* had difficulty feeding on intact *E. kuehniella* eggs. The ability of phytoseiid mites to feed on different food sources depends on the morphology of their mouthparts (Flechtmann and

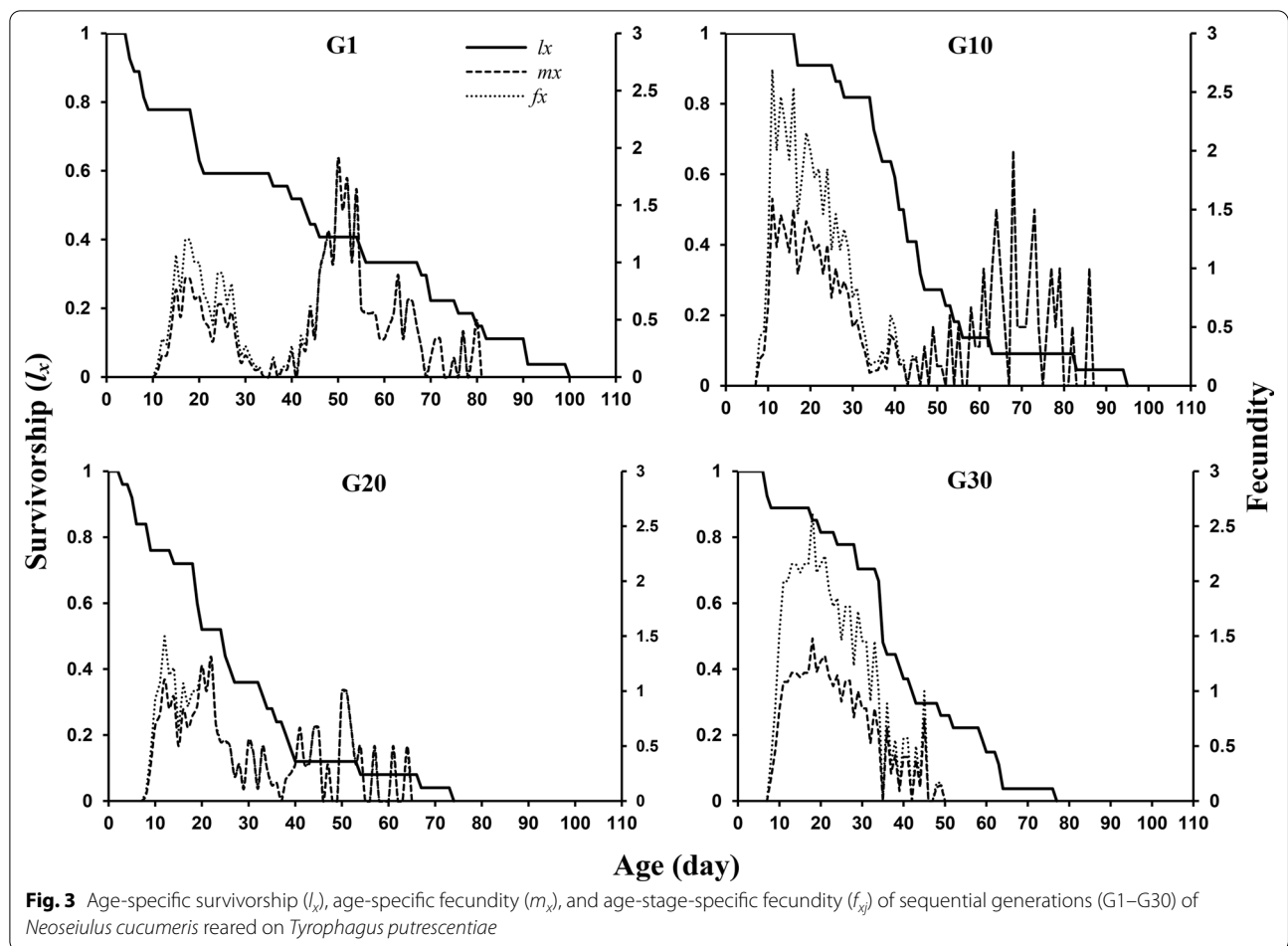
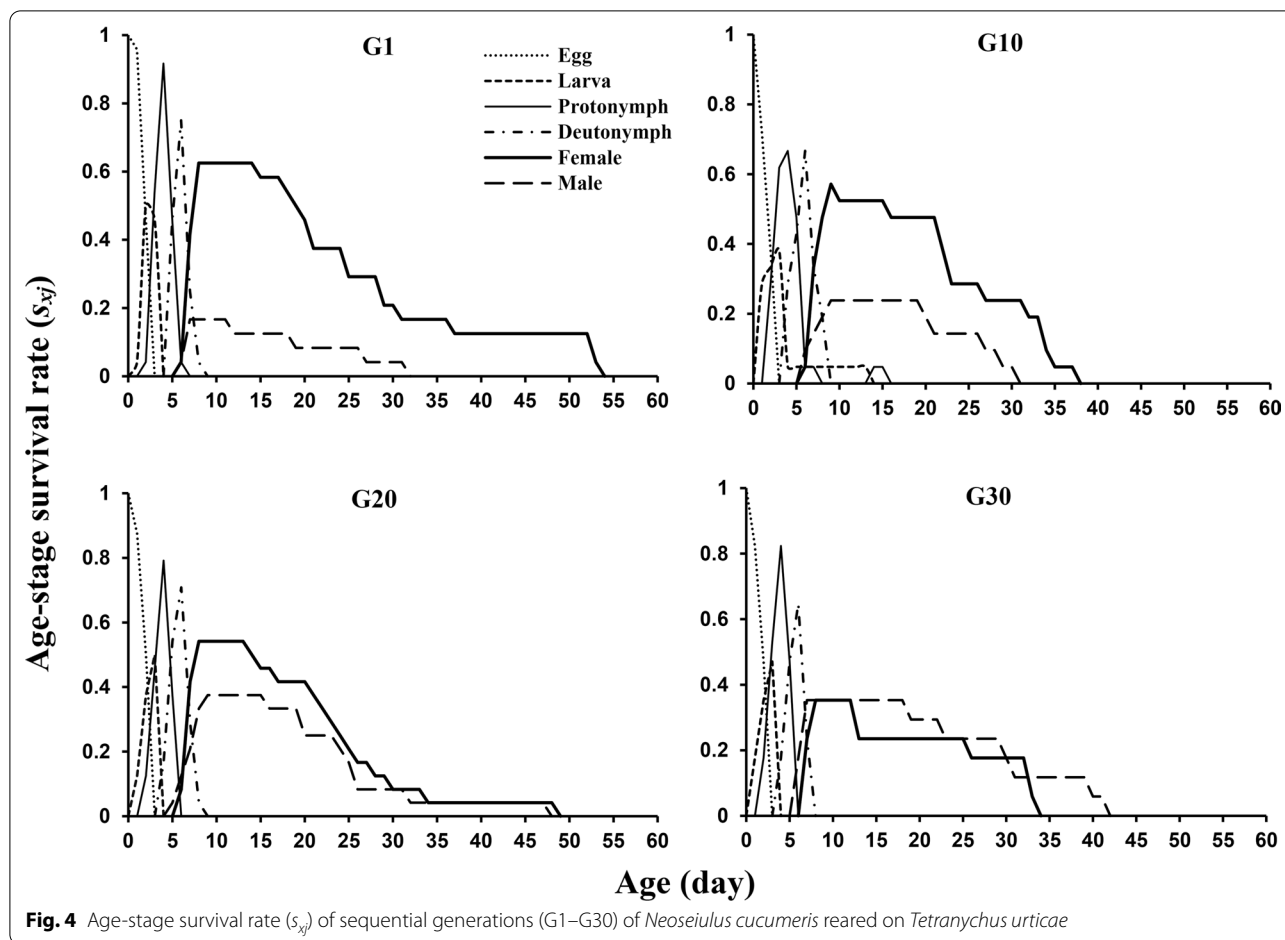


Table 2 Generation-dependent life table parameters (mean \pm SE) of *Neoseiulus cucumeris* reared on *Tyrophagus putrescentiae* and *Tetranychus urticae*

Parameter	<i>Tyrophagus putrescentiae</i>				<i>Tetranychus urticae</i>			
	G1	G10	G20	G30	G1	G10	G20	G30
GRR (eggs/individual)	32.82 \pm 3.377 ^{aA} (32.82)	44.70 \pm 8.981 ^{aA} (46.87)	25.33 \pm 4.771 ^{aA} (25.84)	30.30 \pm 5.442 ^{aA} (30.29)	46.26 \pm 8.960 ^{aA} (46.27)	8.86 \pm 8.869 ^{bB} (8.85)	18.96 \pm 4.327 ^{bA} (18.96)	16.56 \pm 6.281 ^{bA} (16.55)
R_0 (eggs/individual)	15.16 \pm 3.361 ^{abA} (18.38)	26.40 \pm 5.027 ^{abA} (26.41)	10.97 \pm 2.369 ^{ba} (10.96)	23.09 \pm 4.757 ^{aA} (23.07)	18.39 \pm 3.910 ^{aA} (18.37)	6.15 \pm 2.014 ^{bb} (6.14)	12.34 \pm 2.774 ^{abA} (12.33)	8.71 \pm 3.668 ^{abA} (8.71)
r (day ⁻¹)	0.096 \pm 0.010 ^{cB} (0.096)	0.182 \pm 0.013 ^{aA} (0.183)	0.134 \pm 0.015 ^{ba} (0.136)	0.171 \pm 0.014 ^{abA} (0.173)	0.164 \pm 0.012 ^{aA} (0.165)	0.109 \pm 0.023 ^{bb} (0.113)	0.158 \pm 0.015 ^{abA} (0.159)	0.118 \pm 0.030 ^{abA} (0.124)
λ (day ⁻¹)	1.100 \pm 0.011 ^{cA} (1.101)	1.199 \pm 0.016 ^{aA} (1.201)	1.144 \pm 0.017 ^{ba} (1.145)	1.187 \pm 0.016 ^{abA} (1.188)	1.179 \pm 0.014 ^{ab} (1.180)	1.116 \pm 0.026 ^{bb} (1.119)	1.172 \pm 0.017 ^{abA} (1.173)	1.125 \pm 0.033 ^{abA} (1.131)
T (day)	28.24 \pm 1.388 ^{aA} (28.17)	17.94 \pm 0.581 ^{ba} (17.91)	17.69 \pm 0.809 ^{ba} (17.64)	18.24 \pm 0.415 ^{ba} (18.21)	17.58 \pm 0.659 ^{ab} (17.62)	16.05 \pm 0.699 ^{abB} (16.08)	15.69 \pm 0.420 ^{bb} (15.71)	17.37 \pm 1.133 ^{abA} (17.52)

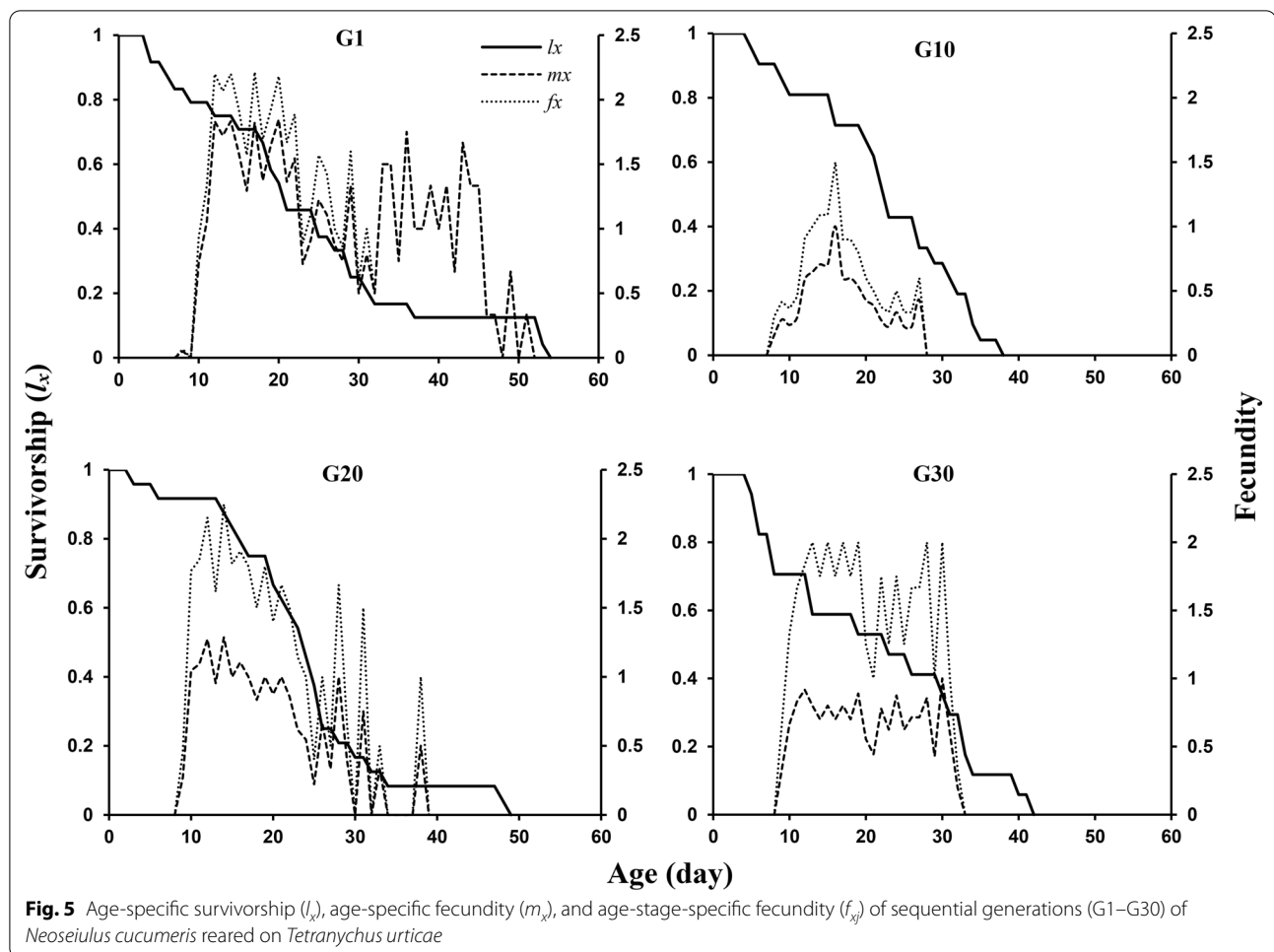
G generation; Data in the first row for each parameter is the mean of the pseudo-values of bootstrap samples (100,000), and data in the parenthesis are their original value. Means followed by different capital letters within the same row are comparisons between corresponding generations of two diets. The means followed by different small letters within the same row are comparisons among different generations of each diet ($P < 0.05$, paired-bootstrap)



McMurtry 1992). Delisle et al. (2015) reported that eggs with a flaw on their outer membrane resulted in more feeding activity. The unfavorable effects of *E. kuehniella* can be related to the resistance of the egg's chorion, anti-feedant factor on the eggs, and the imbalance in the specific nutrients needed for immature development (Riahi et al. 2018). We found *E. kuehniella* eggs are not a suitable food source for *N. cucumeris* due to short adult longevity, long pre-adult duration, high immature mortality, and lack of fecundity. Similarly, *E. kuehniella* eggs did not support the development and survival of *Typhlodromus bagdasarjani* Wainstein and Arutunjan immatures, as none developed beyond the protonymphal stage (Riahi et al. 2018). Conversely, a high level of survival (90% and 88%, respectively) was observed for *N. cucumeris* and *Neoseiulus barkeri* (Hughes) on eggs of *E. kuehniella* (Al-Shemmary 2018). Furthermore, the performance of *N. barkeri* was higher than *Neoseiulus zaheri* Yousef

and El-Borolossy by feeding on the eggs of *E. kuehniella* (Momen and El-Laithy 2007). Momen et al. (2020) evaluated the development and reproduction of *N. barkeri* on *E. kuehniella* and *Mycetoglyphus fungivorus* Oudemans in the first, third, and sixth generations of rearing and concluded that the fecundity and oviposition rate of the predator were higher on *E. kuehniella* than on *M. fungivorus*. Similarly, not only did *N. cucumeris* (Al-Shemmary 2018) and *Amblyseius swirskii* Athias-Henriot (Nemati et al. 2019) oviposit when fed on *E. kuehniella* eggs, but they also showed the highest fecundity on this diet compared to pollen grains and eggs of other insects. In addition, the fecundity of *Neoseiulus californicus* McGregor (Khanamani et al. 2017a) and *A. swirskii* (Riahi et al. 2017a) was high when they were fed on an artificial diet enriched by eggs of *E. kuehniella*.

The shorter development time in *N. cucumeris* reared on *T. putrescentiae* and non-significant differences of



population growth parameters in later generations in the current study indicated that long-term rearing on *T. putrescentiae* led to enhanced performance of the predator. In contrast to our findings on *N. cucumeris*, *T. putrescentiae* was the less favorable factitious prey for *A. swirskii* and *T. bagdasarjani* (Riahi et al. 2017b, 2018). Enrichment of the basic diet provided with this factitious prey with some protein sources resulted in increasing the fecundity of *N. barkeri* (Huang et al. 2013). However, Pirayeshfar et al. (2020) showed that the reproduction of *A. swirskii* was influenced by both the stage and the food substrate used for the rearing of *T. putrescentiae* and they recommended this mite as an excellent alternative food for mass-rearing programs. These inconsistencies may be due to the predator species and different diets used for rearing the acarid mite.

Although most companies in their brochures recommend *N. cucumeris* to control thrips, long-term feeding on *T. urticae* caused no decline in performance and its

predation potential remained high. We suggest *T. urticae* is prey for this predator. The predation rate of females on *T. urticae* was higher than that of males and other stages, especially during the oviposition period. In the current study, the value of C_0 of *N. cucumeris* was 467 prey in G1. However, the value of this parameter was 201 when the predator fed on *T. atlanticus* (Popov and Kondryakov 2008). Furthermore, for the same tetranychid species, this value was 528 prey for *N. californicus* (Khanamani et al. 2017b) and 464 prey for *A. swirskii* (Riahi et al. 2017c). *N. cucumeris* requires a maximum of 49 prey to produce an egg. In contrast, there were 27 and 28 prey for *N. californicus* (Khanamani et al. 2017b) and *A. swirskii*, respectively (Riahi et al. 2017c). Although *N. cucumeris* performs poorly in the dense webbing of spider mites, it showed higher predation on the eggs of *T. urticae* compared with other more specialist predators such as *N. californicus* and *P. persimilis* (Li and Zhang 2016). In conclusion, *N. cucumeris* can be a useful predator against *T.*

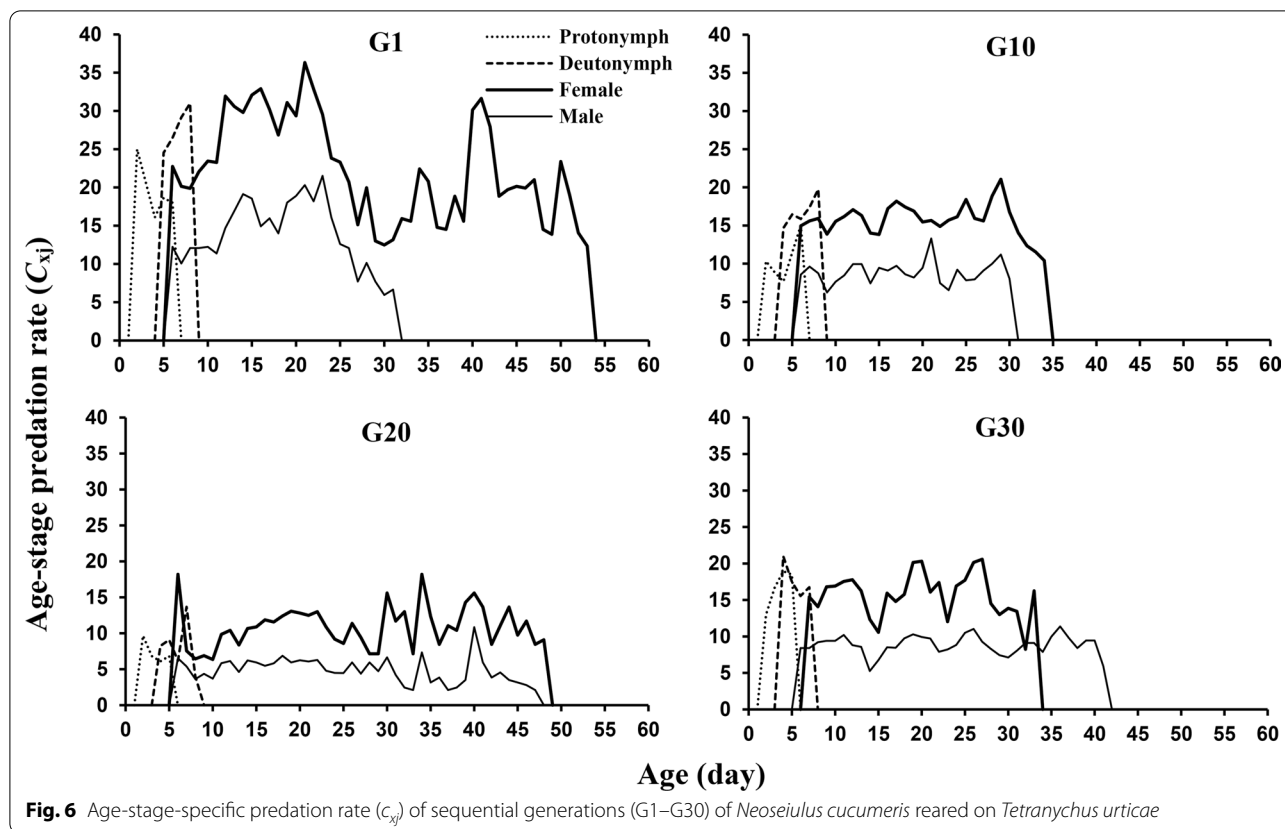


Fig. 6 Age-stage-specific predation rate (c_{xj}) of sequential generations (G1–G30) of *Neoseiulus cucumeris* reared on *Tetranychus urticae*

urticae, especially when the spider mite density is low. Consistent with our findings, Luo et al. (2014) reported successful biocontrol of *T. urticae* by *N. cucumeris*.

The total development time of *N. cucumeris* was significantly shorter on *T. urticae* compared with *T. putrescentiae* in G1. However, there was no significant difference between the two diets at higher generations (G20 and G30). Similarly, the growth rate of *N. cucumeris* was higher when the predator fed on *T. urticae* than on *T. putrescentiae* in G1 but continuing the rearing process resulted in no significant change in reproductive rates between the two diets. This may be due to the lower mobility of *T. putrescentiae* immatures, making them more available to the predator, which conserves energy for the rest of the predator's life. In addition, differences in the nutritional level of the prey and feeding on immotile or motile prey may require different abilities to decode infochemicals and hunt (Dicke et al. 1998). Sarwar et al. (2009) indicated that *N. cucumeris* preferred *T. putrescentiae* followed by *T. urticae*. They concluded that the predator adapted to prey that had been the routine diet for a long time. The non-significant difference in r in the later generations of the current study indicated that *N. cucumeris* accepted natural and factitious prey as diets

for long-term rearing. Although it would be better to rear the phytoseiid mites on the most common natural prey (Goleva and Zebitz 2013; Massaro and de Moraes 2016), it gives rise to high labor costs due to the need for fresh plants for raising prey. Therefore, using *T. putrescentiae* has more practical advantages than using *T. urticae* and could alleviate the problems associated with providing prey mites continuously and facilitate the cost-effective rearing process of *N. cucumeris*.

Conclusions

Our results indicated that *E. kuehniella* eggs were not accepted as food by different life stages of *N. cucumeris* and could not sustain their development and reproduction for at least one generation. On the other hand, the acarid mites, *T. putrescentiae* and *T. urticae* supported the development and reproduction of *N. cucumeris* for more than one generation without any losses in the fitness of this predator after 30 generations. Therefore, *T. putrescentiae* proved to be a suitable cost-effective diet for mass-rearing of *N. cucumeris* because of the high performance of the predator during long-term feeding on this factitious prey.

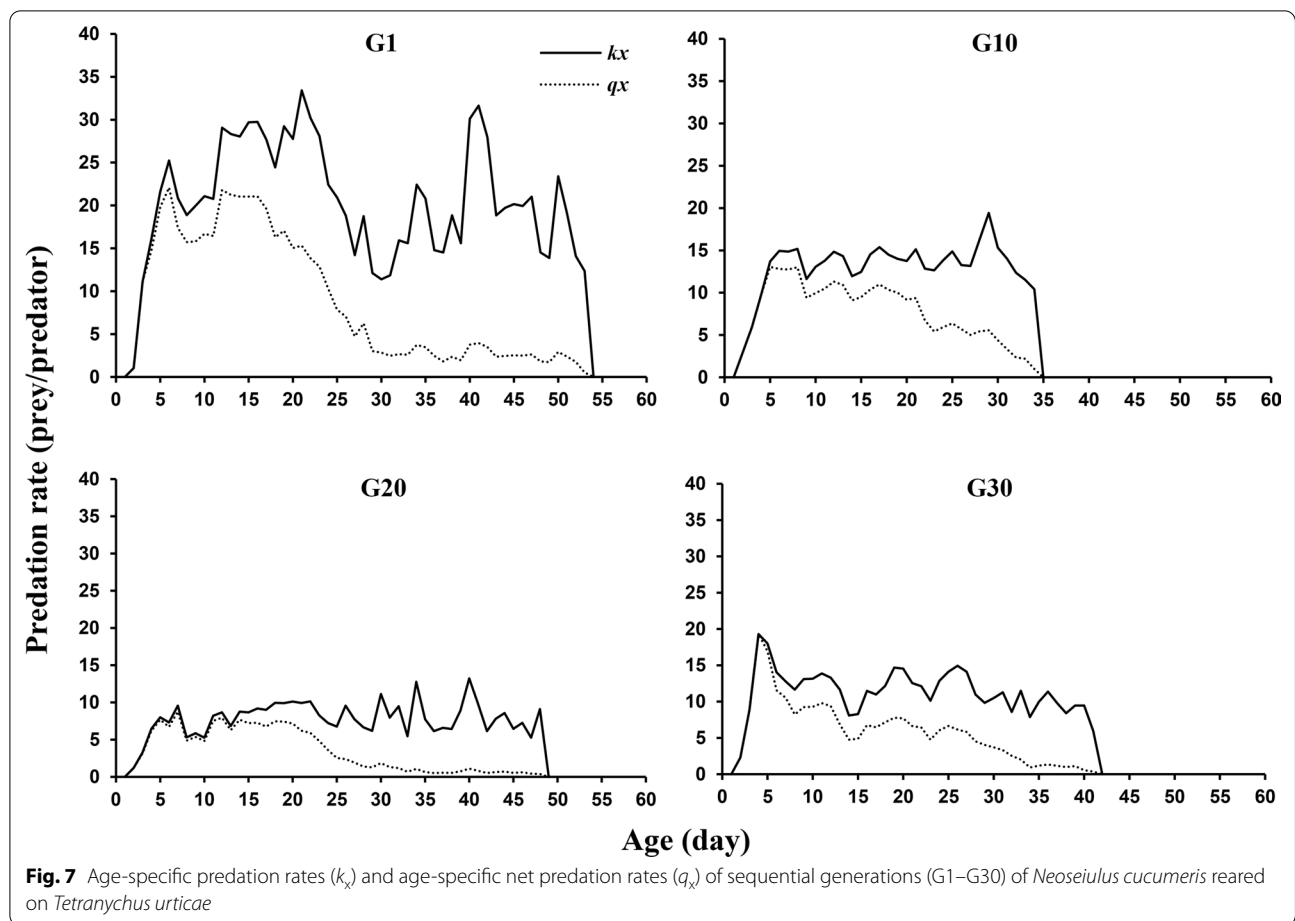


Table 3 Generation-dependent predation rates (mean ± SE) of *Neoseiulus cucumeris* fed on *Tetranychus urticae*

Parameter	G1	G10	G20	G30
Net predation rate (C_0) (prey)	467.48 ± 66.808 ^a	260.35 ± 35.114 ^b	166.34 ± 21.262 ^c	237.88 ± 39.490 ^{bc}
Transformation rate (Q_p) (prey per viable predator egg)	25.89 ± 2.716 ^a	48.85 ± 31.799 ^{ab}	13.93 ± 2.483 ^b	34.39 ± 34.862 ^{ab}
Stable predation rate (ψ) (prey/day)	11.37 ± 0.490 ^a	8.45 ± 0.530 ^b	4.15 ± 0.234 ^c	8.68 ± 0.502 ^b
Finite predation rate (ω) (prey/day)	13.41 ± 0.694 ^a	9.43 ± 0.668 ^b	4.86 ± 0.320 ^c	9.79 ± 0.791 ^b

G generation; the means followed by different letters in the same row are significantly different between treatments using the paired bootstrap test at 5% significance level

Abbreviations

IPM: Integrated pest management; L: Lightness; D: Darkness; RH: Relative humidity; G: Generation; GRR: Gross reproductive rate; R_0 : Net reproductive rate; r : Intrinsic rate of increase; λ : Finite rate of increase; T : Mean generation time; APOP: Adult pre-oviposition period; TPOP: Total pre-oviposition period; s_{xj} : Age-stage survival rate; f_{xj} : Age-stage-specific fecundity of female; l_x : Age-specific survivorship; m_x : Age-specific fecundity; C_0 : Net predation rate; Q_p : Transformation rate; ψ : Stable predation rate; ω : Finite predation rate; c_{xj} : Age-stage predation rate; a_{xj} : Stable age-stage structure.

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Authors' contributions

SY was involved in writing, investigation, data collection and data analysis. YF was involved in supervision, review and editing and project administration. ER was involved in formal analysis, review and editing. MPZ was involved in final review and editing and improvement. All authors read and approved the final manuscript.

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Declarations**Consent for publication**

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Competing interests

The authors declare that they have no competing interests.

Author details

¹Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P. O. Box 14115-336, Tehran, Iran. ²School of Biological Sciences, The University of Queensland, St. Lucia, QLD 4072, Australia.

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