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Experienced generation-dependent functional and numerical responses of *Neoseiulus californicus* (Acari: Phytoseiidae) long-term reared on thorn apple pollen

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Original research

ABSTRACT

The functional and numerical responses of the predatory mite *Neoseiulus californicus* (McGregor) (Phytoseiidae) females reared on thorn apple pollen (*Datura stramonium* L.) over 40 generations on different densities (2, 4, 8, 16, 32, 64 and 128) of deutonymphs of *Tetranychus urticae* Koch (Trombidiformes: Tetranychidae) were determined. The results indicated a type II functional response for *N. californicus* on *T. urticae* in generations of G0 (no rearing on pollen as control), G10, G20, G30, and G40. The attack rate (α) for *N. californicus* females increased as the number of generations increased from G0 (0.079 h^{-1}) to G20 (0.182 h^{-1}), then decreased in G30 and G40. The longest and shortest handling time (T_h) was observed in G0 (1.670 h) and G40 (0.890 h), respectively. The highest value of maximum attack rate (T/T_h) was estimated in G40 (26.96 prey/day). The equation of the regression line showed that the relationship between the prey density and the number of eggs laid was significant in G0, G10 and G40, and the number of eggs deposited by *N. californicus* increased with increasing the density of prey. The relationship between the prey density and ECI (the efficiency of conversion of ingested food) was not significant in tested generations. Our findings show that long-term rearing on thorn apple pollen did not affect the type of functional response and efficiency of *N. californicus* by confirming this predator is an effective biological control agent against *T. urticae*.

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Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch (Trombidiformes: Tetranychidae) is worldwide among the most economically important pests of a variety of crops (Van Leeuwen *et al.* 2015). This phytophagous mite feeds on over 1,100 host plant species including over 150 economic crops (Pavela 2017). Usually, control of phytophagous mites in agricultural systems occurs by chemical pesticides. However, pesticide use has drawbacks including resistance development in target pests, phytotoxicity, secondary pest outbreaks, increased production costs (labor, materials, and equipment), environment pollution, and risks to human health (Fathipour and Sedaratian 2013). Replacing the use of chemical pesticides with eco-friendly

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methods, such as biological control is therefore vital. The use of predaceous mites is one of the more reliable biological control strategies for pests including *T. urticae* (Fathipour and Maleknia 2016; Jafari *et al.* 2010, 2011).

Phytoseiid mites are the most important natural enemies of phytophagous mites (McMurtry *et al.* 1970; Jafari 2010). They are classified into two groups; specialists (types I, II) including oligophagous predators of the tetranychid mites and generalists (types III, IV) that can feed on some phytophagous mites, immature stages of some tiny insects and also plant pollen as a supplementary or alternative food source (McMurtry and Croft 1997; Moraes *et al.* 2004). *Neoseiulus californicus* (McGregor) is one of the important species of phytoseiid mites that is distributed in habitats with high temperature and low humidity (Ahn *et al.* 2010) in Asia, Africa, Europe and North and South America (McMurtry 1977; Moraes *et al.* 2004). It is a type II phytoseiid mite and an effective control agent of *T. urticae* on many crops (McMurtry *et al.* 2013).

Studies of the foraging behaviors of predators helps us to predict their performance in the field and their potential impact on population dynamics of their prey (Jervis *et al.* 1996; Fathipour and Maleknia 2016). A functional response is the number of prey consumed per time unit by predator as a function of prey density (Solomon 1949). Holling (1959) presented three basic types of functional response: linear (I), convex (II), and sigmoid (III). Many predators and parasitoid arthropods have exhibited a type II functional response on their prey, while vertebrate predators which exhibit the type III functional response are regarded as more efficient biocontrol agents (Xiao and Fadamiro 2010; Jafarian *et al.* 2022). Numerical response of predator, the number of offspring produced per time unit at different prey densities by predator, is another component of foraging behavior that can be used to assess a predator's efficiency (Cédola *et al.* 2001; Carrillo and Peña 2012). Functional response and numerical responses of predators may be affected by different factors including temperature (Mohaghegh *et al.*, 2001; Jafari *et al.* 2012), predator's generation (Yazdanpanah *et al.* 2022), density of preys (Cédola *et al.* 2001; Carrillo and Peña 2012), predator age (Fathipour *et al.* 2018; Dalir *et al.*, 2021), host plants of the prey (Madadi *et al.*, 2007; Jafarian *et al.*, 2022), availability of pollen as a supplement to nutritional rescources (Fathipour *et al.*, 2020), the sex of the predator (Parajulee *et al.* 1994) and long-term rearing effects (Castagnoli and Simoni 1999).

Mass rearing of natural enemies for extended time periods or multiple generations has been shown to affect their foraging efficiency and quality (Sørensen *et al.* 2012). Long-term rearing under constant conditions may also lead to the loss of some important characters and result in inbreeding depression, resulting in poor performance of the released individuals at the release time (Sadat *et al.* 2021). Therefore, it is important to be take measures to ensure maintaining biocontrol agent efficacy during the rearing period and before release in the field or in the greenhouse. When the predators are released in the field for biological control, the diet used in the mass-rearing culture influences not only on their predation rate but also their oviposition rates through changes in encounter rate, success ratio, food acquisition, and conversion of food into egg production (Dicke *et al.* 1986; Sabelis and Janssen 1993). Thus, the success of a predator in a biological control program will depend on its efficiency in converting ingested food (ECI) (in number of prey items) into egg biomass (in number of eggs) at different prey densities (Sabaghi *et al.* 2011).

The role of pollen grains as an alternative diet component, and in sustaining the population of phytoseiid mites in the event of prey scarcity is well established (McMurtry and Croft, 1997). Our preliminary tests indicated that among 23 tested pollen grains of different plant species for rearing the *N. californicus,* feeding on *Datura stramonium* (thorn apple) and pistachio pollen grains lead to the best performance in the second generation (Eini *et al.* 2022). In comparison to pistachio, cultivation of *D. stramonium* is relatively easier and from the economic point of view, more pollen grains are obtained from it. Therefore, we studied the life history of *N. californicus* on *D. stramonium* pollen for 40 generations and showed that different life table parameters remained almost constant over this period (Eini *et al.* 2023). In this study, we evaluate the functional and numerical responses of *N. californicus* to *T. urticae* deutonymphs

after long-term rearing on pollen thorn apple at G0, G10, G20, G30 and G40. The results of this research can be used to predict the efficiency of *N. californicus* to control *T. urticae*.

Material and methods

Plants

Bean plants (*Phaseolus vulgaris* L. var. Nine) were cultivated and grown in plastic pots (diameter 20 cm) containing sand, clay and compost (in the ratio of 1:1:1) in a greenhouse in the Faculty of Agriculture, Lorestan University, Iran, at 25±5 °C and 65±10% RH. The plants were watered every three days.

Pollen source

Thorn apple (*Datura stramonium* L.) pollen grains were collected from the garden of medicinal plants at the Faculty of Agriculture, Lorestan University, Khorramabad, Iran, during the Summer of 2019. After drying at 36-38 °C for two days, they were held at -20 and 4 °C for long and short-term storage, respectively (Kolokytha *et al.* 2011).

Stock culture of mites

The initial population of *T. urticae* was collected from bean leaves infested by *T. urticae* from the Faculty of Agriculture, Yasouj University, Kohgiluyeh and Boyer-Ahmad Province, Iran. They were reared on bean plants (*P. vulgaris*) in a greenhouse. Then, the individuals of *T. urticae* were reared on detached fresh bean leaves in a plastic container under laboratory conditions (25±1 °C, 65±5% RH, 16: 8 L: D h). The initial population of the predatory mite *N. californicus* was obtained from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands). Before conducting experiments, the predatory mites were reared for 5 generations on the infested bean leaf discs with different stages of *T. urticae* as prey under laboratory conditions (25±1 °C, 65±5% RH, 16:8 L:D h). Laboratory colonies of *N. californicus* were reared in arenas that consisted of a piece of green plastic sheet (6×4 cm) with short cotton villi on a water-saturated sponge in a plastic container (9×7×4 cm) half-filled with water. The edges of the arena were covered with tissue paper submerged in the water to provide moisture and prevent predators from escaping (Walzer and Schausberger 1999).

Experimental setup

The predatory mite, *N. californicus* was reared on thorn apple pollen for over 40 generations and maintained under laboratory conditions as above. Thorn apple pollen grains were offered ad libitum as the only food source to the predators at every 3 days. The functional and numerical responses of *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40 on *T. urticae* deutonymphs were assessed.

Experimental arenas composed of a 3×3 cm bean leaf disc, were placed on a water-saturated cloth pad in a Petri dish (8 cm diameter). Then, Petri dishes were placed in the middle of a larger Petri dish (10 cm). The edges of the bean leaf disc were covered with wet tissue paper drenched in the water to prevent predators from escaping and to provide a water source. To obtain prey mites of the same age, 150 gravid females of *T. urticae* were randomly taken from the colony and transferred to a bean leaf disc (4 × 7 cm). After 24 h, *T. urticae* females were removed from the arenas. Plastic containers with *T. urticae* eggs were kept and monitored until the emergence of deutonymphs. The newly emerged deutonymphs of *T. urticae* were transferred onto leaf discs with a fine paintbrush (number 000) at densities of 2, 4, 8, 16, 32, 64, and 128 per experimental unit. To obtain same-aged predatory mites, 100 gravid females of *N. californicus* reared on thorn apple pollen were randomly taken from the colony and transferred to a new rearing environment containing pollen. After 24 h, *N. californicus* females were

removed from the arenas. Plastic containers with *N. californicus* eggs were kept and monitored. After emergence of the larva, they were reared on thorn apple pollen to reach adult stage. The newly emerged mated females of the predator (24 h old) after 24 h harvesting, were placed individually in experimental arenas containing different densities of *T. urticae* deutonymphs. This procedure repeated in G0, G10, G20, G30 and G40. After 24 h, the number of prey consumed by each female predator was counted and then predators transferred to new leaf discs without *T. urticae* deutonymphs to determine the numerical response. Then, the total number of eggs laid by the predatory mite over 48 hours was recorded to estimate the numerical response. Fifteen replicates were prepared for each prey density. All experiments were conducted in the laboratory at 25±1 °C, 60±10% RH and 16:8 h L: D photoperiod.

Data analyses

Functional responses were assessed in two steps (Juliano 2001): the logistic regression of the proportion of prey eaten (N_a/N_t) as a function of prey density (N_t) was used to determine the type of functional response (Eq. (1)):

$$\frac{N_a}{N_t} = \frac{exp(P_0 + P_1 N_t + P_2 N_t^2 + P_3 N_t^3)}{1 + exp(P_0 + P_1 N_t + P_2 N_t^2 + P_3 N_t^3)} (1)$$

Where N_a/N_t is the proportion of consumed prey, N_a is the number of killed prey, N_t is the initial number of prey offered, and P_0, P_1, P_2 and P_3 are the intercept, linear, quadratic and cubic coefficients, respectively, estimated using the maximum likelihood method. If the sign of the linear coefficient *(*P_1) being negative ($P_1 < 0$), it implies a type II functional response, whereas If P_1 being positive and P_2 is negative shows a type III functional response (Juliano 2001).

In next step the handling time (T_h) and the attack rate or searching efficiency (a) were estimated by Rogers's random predator equation (Rogers 1972; Hassell *et al.* 1977).

$$N_a = N_t[1 - exp(\alpha(T_h N_a - T))](2)$$

Where N_a is the number of killed prey per experimental unit, N_t is the initial number of prey offered, T is total time available for attack (1 day or 24 h), a is the attack rate, T_h is the handling time of prey by the predator (hours). Nonlinear least-squares regression was used to estimate the attack rate and the handling time parameters (Proc NLIN, SAS Institute, 2003).

In the numerical response experiment, the following equation was used to the efficiency of conversion of ingested food (ECI) into egg biomass at different prey density treatments (Omkar and Pervez 2004).

$$ECI = \frac{\text{Number of eggs laid}}{\text{Number of preys consumed}} \times 100$$

The data on the number of eggs laid by *N. californicus* female and ECI versus prey densities were fitted using regression analysis to determine the relationship between oviposition and ECI of female predators and prey density.

The effects of prey density and predator generation and their interaction on prey consumption and the number of eggs laid were determined using the SAS general linear model (GLM) procedure (SAS Institute, 2003). Tukey's HSD test was used for subsequent pairwise comparisons. The two-way interaction between generation and density was separated by the slicing method (densities at ages and vice versa). This method is a post-ANOVA procedure where a significant interaction term is present and involves breaking the data set into separate parts (Schabenberger *et al.* 2000).

The predator's prey consumption data at different densities of *T. urticae* deutonymphs were regressed linearly against initial prey densities to determine the relationship between the number of consumed prey and prey density. In addition, to determine the relationship between the number of prey consumed and predator generation, the data on prey attacked by predators at

the highest density (128 deutonymphs) versus different predator generations were fitted using both linear and nonlinear regression analyses. The statistical analyses were performed in SAS (version 9.1) and Minitab version 18 (Minitab, 2017).

Results

Functional response

The functional response and percentage of prey consumption of *N. californicus* reared on the thorn apple pollen to different *T. urticae* densities in different generations are presented in Fig. 1. Comparison of the functional response curves demonstrated differences among different tested generations of the predator (Fig 1). The number of *T. urticae* killed per day increased with increasing prey density from 2 to 128. The percentage of consumed *T. urticae* deutonymphs decreased as the prey density increased in all tested generations (Fig 1). The linear coefficient of equation 1 (P_1) in results of logistic regression analysis for predator in all tested generations was negative, indicating a type II functional response (Table 1). With increasing the number of generations from G0 (0.079 h^{-1}) to G20 (0.182 h^{-1}), α values increased, then decreased in G30 (0.040 h^{-1}) and G40 (0.034 h^{-1}) (Table 2). The T_h values ranged among generations: decreased from G0 to G10, then increased to G30, and declined again in G40. The longest (1.670 h) and shortest handling time (T_h) (0.890 h) were observed in G0 and G40, respectively. The highest (26.96 prey/day) and lowest (14.371 prey/day) estimated T/T_h for a female of *N. californicus* on *T. urticae* were observed in G40 and in G0, respectively (Table 2).

Table 1 Results of logistic regression analysis of *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40 to the proportion of different densities of *T. urticae* deutonymphs.

Generation	Parameter	Estimate ±SE	χ^2	*P*
G0	Constant (P_0)	1.476±0.244	36.43	<0.0001
	Linear (P_1)	-0.095±0.018	26.68	<0.0001
	Quadratic (P_2)	0.0010±0.0003	8.93	0.0028
	Cubic (P_3)	$-4.08\times 10^{-6} \pm 1.741 \times 10^{-6}$	5.48	0.0192
G10	Constant (P_0)	2.825±0.284	98.43	<0.0001
	Linear (P_1)	-0.1827±0.021	74.01	<0.0001
	Quadratic (P_2)	0.00258±0.0003	42.39	<0.0001
	Cubic (P_3)	$-0.00001\pm 1.941\times 10^{-6}$	33.94	<0.0001
G20	Constant (P_0)	1.9589±0.240	66.57	<0.0001
	Linear (P_1)	-0.0914±0.017	26.80	<0.0001
	Quadratic (P_2)	0.000860±0.000334	6.63	0.0101
	Cubic (P_3)	$-3.16\times 10^{-6} \pm 1.661\times 10^{-6}$	3.63	0.0568
G30	Constant (P_0)	2.893±0.269	115.61	<0.0001
	Linear (P_1)	-0.245±0.021	129.07	<0.0001
	Quadratic (P_2)	0.00387±0.000412	88.22	<0.0001
	Cubic (P_3)	$-0.00002\pm 2.036\times 10^{-6}$	74.85	<0.0001
G40	Constant (P_0)	1.075±0.213	25.35	<0.0001
	Linear (P_1)	-0.095±0.016	33.09	<0.0001
	Quadratic (P_2)	0.0014±0.000318	20.16	<0.0001
	Cubic (P_3)	$-6.63\times 10^{-6}\pm 1.581\times 10^{-6}$	17.58	<0.0001

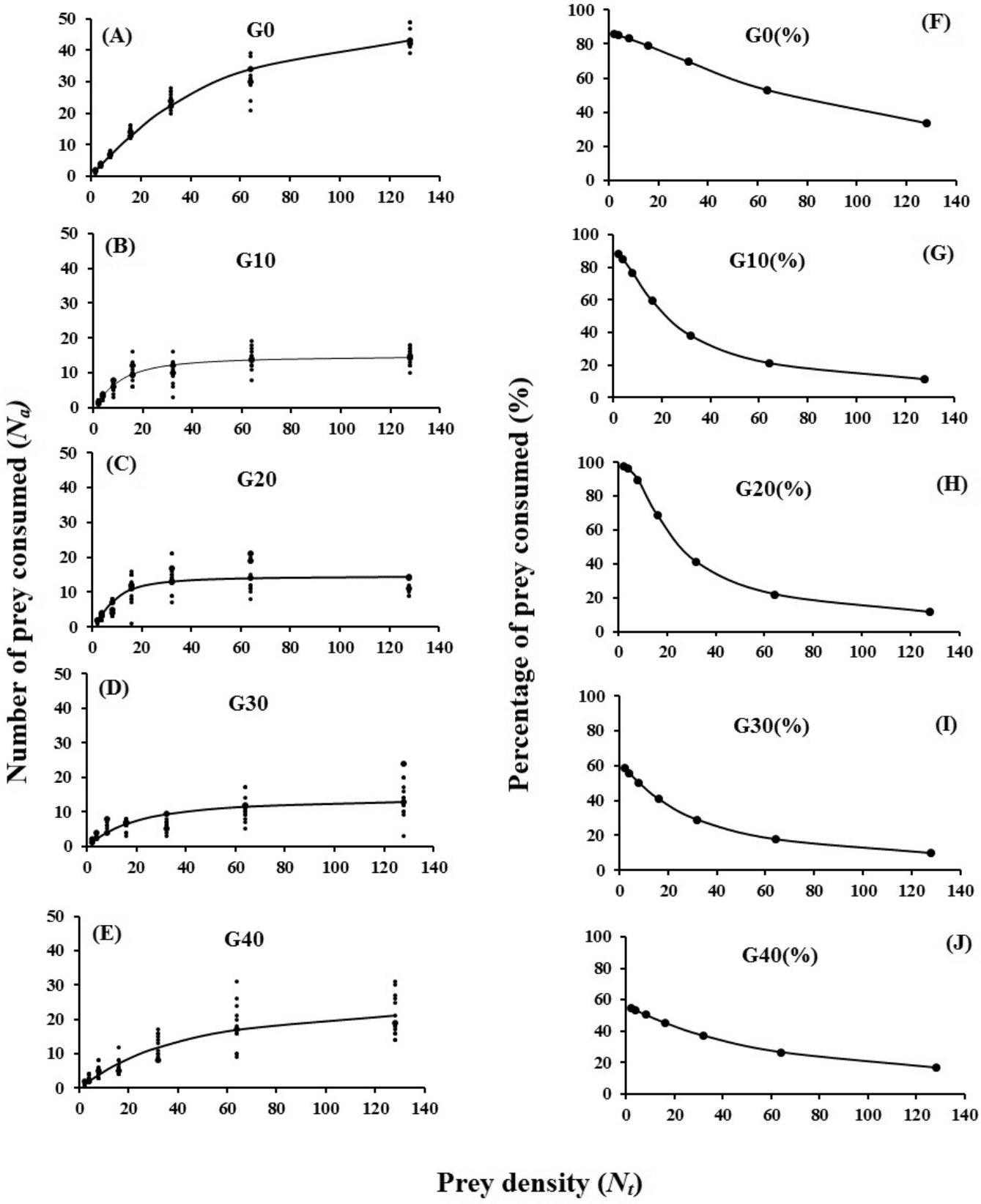

Figure 1 Functional response (A-E) and percentage of prey consumed (F-J) curves by adult females of *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40 to different densities of *T. urticae* deutonymphs.

Table 2 Estimated (±SE) attack rate (a), handling time (T_h) and estimated maximum attack rate (T/T_h) of *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40 to different densities of *T. urticae* deutonymphs. The values in parentheses represent 95% confidence intervals.

Generation	a (h^{-1})	T_h (h)	T/T_h (prey/d)	R^2
G0	0.079± 0.017 (0.044-0.114)	1.670±0.090 (1.491-1.850)	14.371	0.919
G10	0.102±0.019 (0.063-0.141)	1.594±0.065 (1.465-1.724)	15.056	0.944
G20	0.182±0.062 (0.059-0.305)	1.611±0.087 (1.436-1.785)	14.897	0.909
G30	0.040±0.008 (0.022-0.057)	1.658±0.130 (1.40-1.917)	14.475	0.856
G40	0.034±0.005 (0.024-0.045)	0.890±0.072 (0.746-1.033)	26.960	0.913

Estimating the predation capacity

The effects of prey density and predator generation on the predation rate of *N. californicus* on *T. urticae* deutonymph, as well as the interaction between them were significant. There was a significant difference among seven offered prey densities in every generation (Table 3). In almost all generations, the consumption rate increased with increasing the prey density (Table 4). In most generations, the highest mean consumption rate was observed at densities of 64 and 128 (Table 4). The lowest and highest number of prey consumed by *N. californicus* were observed at density of 2 in G10 (1.50 prey) and at density of 128 in G40 (20.73 prey), respectively (Table 4). There was no significant difference in daily consumption of predator at densities of 2, 4 and 8 among generations, but in other densities the consumed prey among generations was different (Table 4).

Numerical response

The results of linear and nonlinear regression analyses of the relationship between the prey density and eggs laid and ECI in different generations of *N. californicus* are shown in Figure 2. The relationship between the prey density and eggs laid in G0, G10 and G40 was significant, and the number of laid eggs increased with increasing the density. The relationship between the number of eggs laid and the prey density was linear in G10, whereas it was nonlinear in G0 and G40. The relationship between the prey density and ECI was not significant in all tested generations (Fig 2).

GLM procedure indicated that predator generation, prey density and interaction between them significantly affected the eggs laid (Table 5). The interaction effects between predator generation and prey density on the number of eggs laid was shown in table 6. In all tested generations, a significant difference was observed between different densities in the oviposition

Table 3 Analysis of variance for the effects of predator generation and prey density on predation rate of *N. californicus* of *T. urticae* deutonymphs after long term rearing on thorn apple pollen.

Source	*df*	*MS*	*F*	*P*
Generation	4	80.344	8.83	<0.0001
Prey density	6	1773.710	194.85	<0.0001
Generation × Prey density	24	60.876	6.69	<0.0001
Error	440	9.102	-	-

Table 4 Prey consumed (means± SE) at different *T. urticae* deutonymph densities by *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40. Vertical means (lowercase letters) and horizontal means (capital letters) followed by different letters are significantly different ($P \leq 0.05$, Tukey's test).

Experimental factors	Predator generation				
Prey density	0	10	20	30	40
2	1.66±0.142^{aE}	1.50±0.202^{aD}	1.85±0.097^{aD}	1.66±0.125^{aE}	1.58±0.148^{aD}
4	2.70±0.163^{aDE}	3.15±0.317^{aD}	3.35±0.199^{aCD}	3.33±0.186^{aDE}	3.07±0.239^{aCD}
8	5.72±0.506^{aCD}	6.64±0.464^{aC}	5.73±0.556^{aC}	6.80±0.553^{aC}	4.85±0.455^{aCD}
16	8.71±0.766^{abBC}	10.20±0.738^{aB}	11.26±1.053^{aB}	6.28±0.437^{bCD}	6.07±0.635^{bC}
32	11.00±1.043^{abAB}	10.00±1.007^{bB}	14.26±1.030^{aAB}	6.07±0.459^{cCD}	11.40±0.882^{abB}
64	12.46±1.008^{bA}	14.07±0.787^{abA}	14.91±1.384^{abA}	10.86±0.855^{bB}	18.07±1.791^{aA}
128	13.76±1.013^{bA}	14.80±0.633^{bA}	11.88±0.734^{bAB}	14.64±1.598^{bA}	20.73±1.458^{aA}

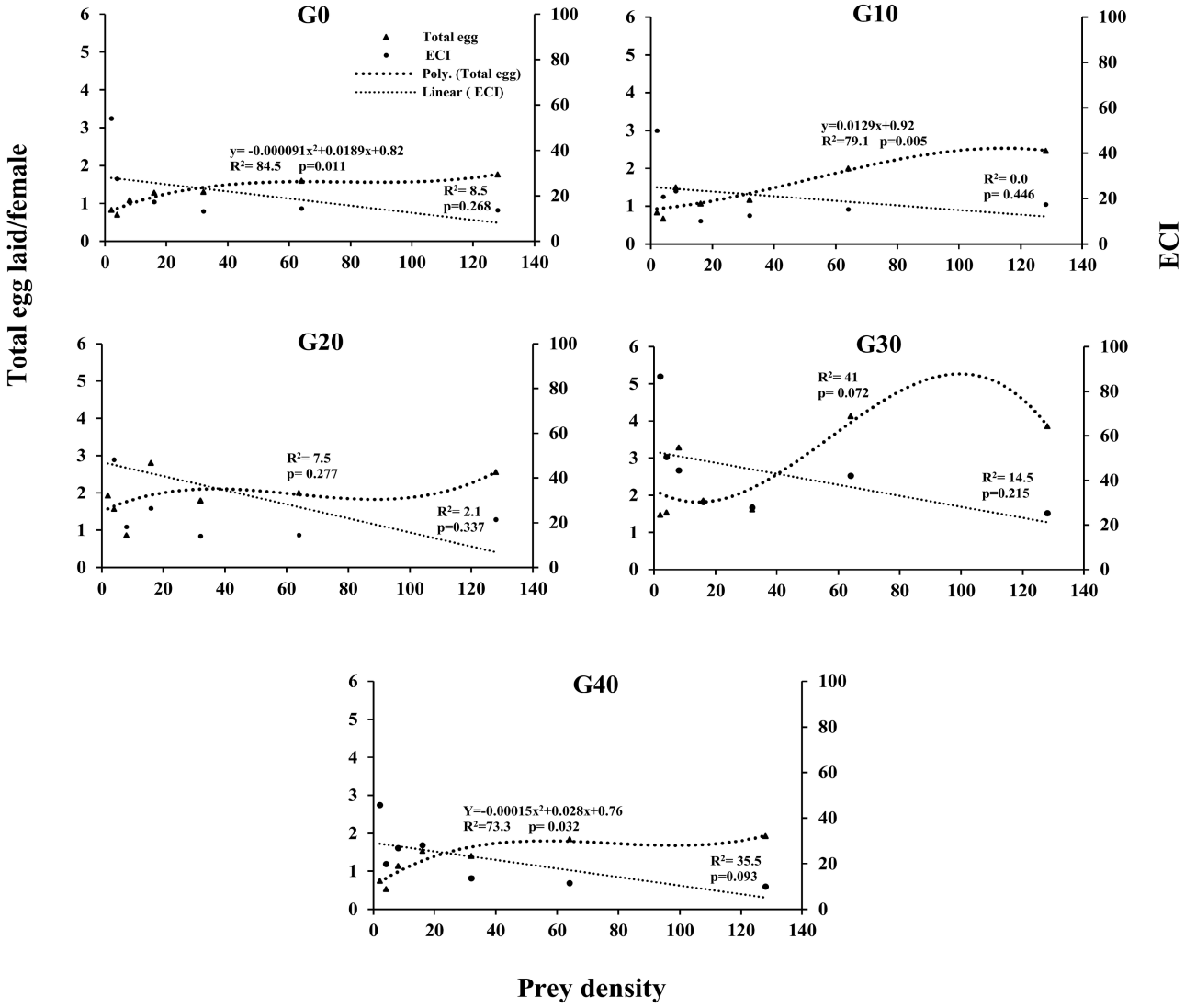

Figure 2 The relationship between the number of eggs laid and ECI of *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40 in different densities of *T. urticae* deutonymphs.

Table 5 Analysis of variance for the effects of predator generation and prey density on oviposition of *N. californicus* reared on thorn apple pollen in G0, G10, G20, G30 and G40 at different densities of *T. urticae*.

Source	*df*	*MS*	*F*	*P*
Generation	4	29.422	24.83	<0.0001
Prey density	6	20.404	17.22	<0.0001
Generation × Prey density	24	3.782	3.19	<0.0001
Error	436	1.185	-	-

rate of *N. californicus*, except for the G0. In addition, the laid eggs increased with increasing density of the prey in all generations (Table 6). There was no significant difference in densities of 4 and 32 deutonymph density in all generations tested (Table 6). But at other densities, significant differences were observed in different generations. So that the highest number of eggs laid by *N. californicus* were observed at a density of 64 and 128 per G30 (Table 6).

Discussion

Functional response experiments have been frequently used to characterize and compare the effectiveness of biological control agents. These indicate that a Type II functional response is common in predators belonging to the family Phytoseiidae including: *Amblyseius swirskii* Athias-Henriot (Fathipour *et al.* 2020), *Neoseiulus cucumeris* (Oudemans) (Shipp and Whitfield 1991; Yazdanpanah *et al.* 2022), *Iphiseius degenerans* Berlese (Eveleigh and Chant 1981), *Neoseiulus barkeri* Hughes (Jafari *et al.* 2011), *Galendromus occidentalis* (Nesbitt) (Laing and Osborn 1974), *Phytoseiulus longipes* Evans (Badii and McMurtry 1988) and *Phytoseiulus persimilis* Athias-Henriot (Laing and Osborn 1974; Everson 1979; Eveleigh and Chant 1981; Skirvin and Fenlon 2001), *N. californicus* (Pereira de Sousa Neto *et al.* 2019; Khanamani *et al.* 2017; Ahn *et al.* 2010; Cédola *et al.* 2001), *Typhlodromus bagdasarjani* Wainstein & Arutunjan (Jafarian *et al.* 2022). Our results confirmed the type II functional response of *N. californicus* to deutonymphs of *T. urticae* in five tested generations. In addition, the results showed mass rearing on thorn apple pollen for 40 generations did not affect the type of functional response in the face of *T. urticae*. This type of functional response suggests that the percentage of killed prey by the predator is inversely related to prey density and this predator would be more efficient at low or moderate densities of *T. urticae* deutonymphs. These findings are consistent with those reported by Khanamani *et al.* (2017), who indicated a type II functional response for *N. californicus* reared over 20 generations on almond pollen to deutonymphs of *T. urticae*.

Table 6 The number of eggs laid (±SE) by *N. californicus* reared on thorn apple pollen at different *T. urticae* densities in G0, G10, G20, G30 and G40. Vertical means (lowercase letters) and horizontal means (capital letters) followed by different letters are significantly different ($P \leq 0.05$, Tukey's test).

Experimental factors	**Predator generation**				
Prey density	**0**	**10**	**20**	**30**	**40**
2	0.83 ± 0.207^{bA}	0.83 ± 0.207^{bBC}	1.92 ± 0.245^{aAB}	1.46 ± 0.290^{abB}	0.75 ± 0.278^{bB}
4	0.70 ± 0.260^{aA}	0.66 ± 0.188^{aC}	1.57 ± 0.250^{aAB}	1.53 ± 0.350^{aB}	0.53 ± 0.243^{aB}
8	1.09 ± 0.284^{bA}	1.50 ± 0.291^{bABC}	3.28 ± 0.285^{aB}	3.28 ± 0.285^{aA}	1.14 ± 0.231^{bAB}
16	1.28 ± 0.265^{bA}	1.06 ± 0.228^{bBC}	2.80 ± 0.427^{aA}	1.85 ± 0.253^{abB}	1.53 ± 0.243^{bAB}
32	1.30 ± 0.286^{aA}	1.16 ± 0.228^{bBC}	1.80 ± 0.311^{aAB}	1.61 ± 0.266^{aB}	1.40 ± 0.254^{aAB}
64	1.60 ± 0.254^{bA}	2.00 ± 0.277^{bAB}	2.00 ± 0.325^{bAB}	4.13 ± 0.290^{aA}	1.84 ± 0.191^{bA}
128	1.76 ± 0.302^{bA}	2.46 ± 0.466^{abA}	2.55 ± 0.376^{abA}	3.85 ± 0.512^{aA}	1.93 ± 0.228^{bA}

Sometimes the functional response of phytoseiid mites may change from type II to type III in response to morphological characters of the host plant (Skirvin and Fenlon 2001), temperature (Skirvin and Fenlon 2003), prey stage (Ganjisaffar and Perring 2015), age of predator (Dalir *et al.* 2021) and prey species (Escudero and Ferragut 2005).

The attack rate (a) and handling time (T_h) coefficients help us to assess the magnitude of functional responses (Pervez and Omkar 2006). Our results show that with increasing number of generations from G0 to G20 the attack rate (α) increased, then it began to decrease. Handling time provides information about the efficiency of a predator, as well as reflects the cumulative time spent to capture, kill, and digest the prey (Holling 1959). The handling time values were different in tested generations. The longest and shortest handling times were recorded in G0 and in G40 respectively, indicating that *N. californicus* spent less time resting or doing other activities such as hunting after mass rearing on pollen in G40, which suggest that predators could consume more prey in each time interval. According to our results, by continuing the mass-rearing process the predator recovered its efficiency, as shown by a decrease in handling time. Yazdanpanah *et al.* (2022) showed that the handling time of *N. cucumeris* decreased with mass-rearing up to 20 generations and then increased in G30. Behavioral changes in natural enemies under long-term rearing may occur due to environmental or genetic adaptability (Evenden *et al.* 2002). When the phytoseiids were transferred to a new diet, they were presumably not identical with respect to satiation levels, because the previous food, even though it had been supplied ad libitum, did not have the same nutritional quality. In fact, *N. californicus* shows different rates of increase when continuously fed on each of these food types (Castagnoli and Simoni 1991). Furthermore, a phytoseiid subjected to any change needs some time to adapt to the new condition (Castagnoli *et al.* 2001). In G20 *N. californicus* reared on the thorn apple pollen showed the highest attack rate (a) (0.182 prey/d) with a handling time of 1.611 h. But Khanamani *et al.* (2017) showed the attack rate and handling time of *N. californicus* reared on the almond pollen was 0.114 (prey/d) and 0.333 (h), respectively in G20, differently from our results. The difference between these findings may be due to the differences in nutritional histories of the predator, rearing techniques, the quality of the pollen used, difference in genetic populations, the difference in age and stage of the tested predator, and differences in the quality of *T. urticae* used as food.

Similar to our findings, Yazdanpanah *et al.* (2022) showed that the relationship between the ECI of female predator and prey density was not significant in all tested generations. Our findings showed a significant relationship between the number of eggs laid by *N. californicus* and the density of *T. urticae* deutonymphs in G0, G10 and G40. The oviposition rate of phytoseiid mites is related to predation because they always devote a major fraction of food ingested to egg production (Sabelis and Janssen 1994). The relationship between the number of eggs laid and the prey density was linear in G10 and the number of eggs increased by increasing the prey number; the rate of oviposition rapidly increased with increasing prey density in G0 and G40 and the relationship between them was nonlinear, with increasing rate slow at higher densities. The plateau of oviposition rate of predatory mites at high prey densities is possibly due to the satiation of the nutrient constraints for egg production and the limitation of females to lay not more than a certain number of eggs at high prey densities (Omkar and Pervez 2004; Fathipour *et al.* 2020). Considering that this predator is nutritionally type II (capable of controlling two-spotted spider mites on various crops), it can also consume other mite species, small insects, or pollen when the primary prey is unavailable (McMurtry and Croft 1997). The differences observed over generations can be explained by the food habits of the predator because long-term rearing of biological agents on alternative foods may alter their different physiological and behavioral properties including foraging behaviors and the predation rate of the reared biocontrol agents under constant conditions may be influenced when exposed to the main prey (Pratissoli *et al.* 2004; Ansari Shiri *et al.* 2022; Castagnoli and Simoni 1999). The results of these findings in G0 and G40 are similar to those reported for *N. californicus* on *T. urticae* (Khanamani *et al.* 2017) and for *A. swirskii* on *T. urticae* (Bazgir *et al.* 2020). Furthermore, there was a significant relationship between predator generation and prey density

on oviposition of *N. californicus*: after long-term rearing (40 generations) of *N. californicus* on thorn apple pollen, the oviposition rate at all densities is not significantly different between G0 and G40. Therefore, the thorn apple can be a suitable alternative food for the long-term rearing of *N. californicus*.

Our findings suggested that mean prey consumption of *N. californicus* increased with increasing prey density in all generations. Our results also indicated that at the highest prey density in all generations, there was a significant difference between the G40 and other generations. On the other hand, the results showed the longest handling time was recorded in G0 (1.670 h), G3 (1.657 h), G20 (1.611 h), and G10 (1.594 h), showing a lower mean consumption rate than G40 (0.890 h) at the higher prey densities. The results of these findings are similar to those observed for *N. cucumeris* on eggs of *T. urticae* (Dalir *et al.* 2021), *N. cucumeris* on nymphs of *T. urticae* (Yazdanpanah *et al.* 2022) *N. californicus* on *T. urticae* (Zheng *et al.* 2017), *A. swirskii* on *T. urticae* in presence and absence of pollen (Fathipour *et al.* 2020).

The long-term rearing of the predator on alternative foods and supplementary diet is one of the influencing factors on the functional response (Fathipour *et al.* 2020; Khanamani *et al.* 2017). Also, Sarwar *et al.* (2009) indicated that the predator has adapted to the prey that has been its usual diet for a long time. Our findings show that long-term rearing on thorn apple pollen did not affect the type of functional response of *N. californicus*, but could affect the number of eggs laid and the number of prey consumed. However, the efficiency of the predator mite was not significantly different in the first and last generations. *Neoseiulus californicus* could be an efficient biocontrol agent of *T. urticae* in long-term rearing on thorn apple pollen under controlled conditions. However, more research such as greenhouse studies are needed to investigate the efficacy of mass-reared predators under natural conditions.

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