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Research Article

Temperature-dependent functional response of the predatory mite *Neoseiulus californicus* (Acari: Phytoseiidae) on *Tetranychus urticae* (Acari: Tetranychidae)

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Abstract: Investigating the functional response of natural enemies across temperatures is essential for assessing their efficacy in biocontrol programs. Therefore, the functional response of *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) was assessed on the larvae and protonymphs of *Tetranychus urticae* (Koch) (Acari: Tetranychidae) at seven constant temperatures of 10, 15, 20, 25, 30, 32.5, and 35 ± 1 ℃. At each temperature, the experiments were carried out at seven prey densities of 2, 4, 8, 16, 32, 64, and 128 larvae and protonymphs. Logistic regression showed a type III functional response at 10, 15, 20, and 25 °C, but a type II response at the other temperatures tested. The attack rate (*a*) and attack coefficient (*b*) increased with increasing temperature; therefore, the highest *b* (0.00777 h^{-1}) and *a* (0.2329 h^{-1}) were estimated at 25 and 35 °C, respectively. The highest attack rate over 24 h and the shortest handling time (T_h) were recorded at 30 °C. Prey density and temperature significantly affected the predation rate of N. californicus on *T. urticae*; however, their interaction was not significant. At all temperatures tested, consumption increased with increasing prey density. At the highest prey density (128 individuals), the maximum consumption rate was observed at 30 ℃. Assessing the functional response and predation capacity of *N. californicus* on T. urticae larvae and protonymphs demonstrates its potential as an effective biocontrol agent against this mite pest, particularly at temperatures above 25 °C.

Keywords: Attack rate, Consumption rate, Handling time, Prey-predator interactions, *Tetranychus urticae*

Introduction

Integrated Pest Management (IPM) is widely recognized today as an effective strategy for selecting and implementing the most efficient control tactics. Biological control is a fundamental component of IPM (Francis *et al.*, 2020; Jakubowska *et al*., 2022). Identifying effective biological control agents is the initial step in developing successful biological control programs. A key method for assessing predator efficiency involves analyzing life table

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parameters and foraging behaviors. These parameters enable better comparisons and selections for biological control strategies (Fathipour and Maleknia 2016).

To assess predator foraging behavior, researchers use a key tool called the functional response (Yazdanpanah and Fathipour 2026). This describes the functional response of a natural enemy, which characterizes how the predator's consumption rate changes with varying prey densities. The functional response is a commonly measured attribute of natural enemies (Hassell 1978). There are three common types of functional responses: a linear predation rate that levels off at a constant plateau (type I), a hyperbolic or decelerating curve (type II), and a sigmoid (type III) (Pervez 2005; DeLong 2021). Predator effectiveness is closely linked to the nature of its functional response; however, various biotic and abiotic factors can affect it (Parajulee *et al., 2*006).

Temperature is an important abiotic factor that affects foraging characteristics (Vasseur and McCann 2005). This factor can change prey and predator behavior and physiology, affecting their interactions (Diamond 2018). At times, temperature fluctuations can change the rate at which predators consume prey, as this is influenced by changes in the predator's metabolic rate, resulting in a shift in the type of functional response (De Clercq *et al., 2*000; Jalali *et al., 2*010). Therefore, understanding temperature-dependent functional responses is essential for predicting predator performance under varying environmental conditions. Several studies have examined phytoseiid mites. For example, the functional responses of *Amblyseius swirskii* (Athias-Henriot), *Neoseiulus barkeri* Hughes, and *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) to the predation of different life stages of *Tetranychus urticae* (Koch) have been examined at different temperatures. In these studies, each species showed different responses to temperature changes (Skirvin and Fenlon, 2003; Jafari *et al., 2*012; Afshar and Latifi 2017), suggesting that temperature-dependent responses vary between species (Walker *et al., 2*020). Such interspecific variation highlights the importance of evaluating each predator species individually.

Among these species, *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) is recognized as an efficient predatory mite. It has been successfully used for biological control of agricultural pests (Ahn *et al*., 2010). This predator prefers to feed on mites in the family Tetranychidae (Fathipour and Maleknia, 2016). Within this family, *T. urticae* is one of the most economically important species and can cause severe damage to a wide range of crops. Because of its high reproductive rate, short life cycle, and ability to develop resistance to chemical pesticides, its management is challenging; therefore, implementing integrated pest management (IPM) strategies, including biological control, is essential (El-Sayed *et al*., 2022).

Although predation efficiency may vary under different environmental conditions, *N. californicus* has been shown to maintain predation on multiple mite species and life stages, demonstrating flexibility in prey utilization and survival even under fluctuating temperatures (Chen *et al., 2*022; Busuulwa *et al., 2*025). Despite this, understanding how both predator and prey respond to temperature is essential for pest management programs; however, comprehensive research on the functional response of N. californicus when feeding on T. urticae larvae and protonymphs at different temperatures remains limited.

Materials and Methods

Prey and predator rearing

The original *T. urticae* population was collected from a rose greenhouse in Golzar, Tehran, Iran, in 2021. The rose leaves were harvested and brought to the laboratory. The mites were collected with a fine, soft-pointed brush and placed on the leaves of bean plants (*Phaseolus vulgaris* var. Khomein). The two-spotted spider mites were raised on bean plants at 25 ± 5 °C, 65 ± 10% RH, and a photoperiod of 16:8 (L:D) h under greenhouse conditions.

The *N. californicus* colony was provided by BioBest, Belgium (Californicus-System®) in

2021. The colony of predators was retained in arenas consisting of a green plastic sheet (13 × 11 × 0.1 cm) on water-saturated foam in a plastic box (21 × 21 × 9.5 cm) that was half-filled with water. All margins of the green sheet were covered with a 1-cm-wide band of cotton to prevent predators from escaping. To mimic a natural habitat as closely as possible, we placed a few cotton strands on the plastic arenas as shelter and oviposition sites. Maize pollen (*Zea mays* L.) collected from maize fields in Pakdasht, Tehran province, was added as supplementary food by brushing onto the plastic sheets every 3 days. Individuals were reared in growth chambers at 25 ± 1 °C, 65 ± 5% RH, and a photoperiod of 16:8 (L :D) h.

Functional response

To obtain same-aged predatory mites, some gravid females of *N. californicus* were randomly transferred from the colony to new arenas before experiments. The arenas included a bean leaf disc (approximately 6 cm diameter) with all life stages of the two-spotted spider mite, placed upside down on a thin layer of wet cotton, inside a plastic Petri dish (8 cm in diameter, 1 cm height). Moistened cotton strips were used around the edges of leaf discs to prevent predator mites from reaching their prey. A few cotton strands were placed in the center of leaf disc as an oviposition site. We put fine mesh on the lid of each Petri dish for ventilation. After 24 h, *N. californicus* females were removed from the arenas. A Petri dish containing *N. californicus* eggs was maintained at 25 ± 1 °C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h, and observed. The first instar of female predators was chosen and utilized for the experiments. For this experiment, an approximately 4 cm diameter bean leaf cut was placed upside down on water-saturated cotton inside a small petri dish (6 cm diameter), as described above. The offered densities of two-spotted spider mites from larvae and protonymphs were 2, 4, 8, 16, 32, 64, and 128. To ensure that the *T. urticae* gravid females were of the same age, two-spotted spider mite females were transferred onto the leaf cut using a thin brush and permitted to lay their eggs. After 24 h, the adult females were removed. We maintained and monitored eggs until larvae and protonymphs emerged. They were then used as prey in the assay. The functional response experiments were conducted with 24 h-starved, 1-day -old females. Each experimental unit included one starved female predator. After 24 h, the females were removed and the predation was estimated in terms of the number of mites attacked per female. We tested the functional response of *N. californicus* at seven temperatures (10, 15, 20, 25, 30, 32.5, and 35 °C) under 65 % RH and a 16:8 (L:D) h photoperiod. All densities were replicated 12 times at each temperature.

Statistical analysis

The analysis of the functional response was conducted in two stages. In the initial phase, the type of functional response and the parameters of the functional response curve were assessed through a logistic regression of the proportion of prey consumed (N_a/N_0) in relation to prey density (Equation 1):

$$\frac{N_a}{N_0} = \frac{exp(P_0+P_1N_0+P_2N_0^2+P_3N_0^3)}{1+\exp(P_0+P_1N_0+P_2N_0^2+P_3N_0^3)} \quad \text{(Equation 1)}$$

In this context, P_0, P_1, P_2, and P_3 represent the maximum likelihood estimates of the constant, linear, quadratic, and cubic coefficients in the regression model, respectively. By examining the signs of P_1 and P_2 from Equation 1. we can identify the type of functional response. A scenario where $P_1 < 0$ indicates a type II functional response, while if $P_1 > 0$ and $P_2 < 0$, it indicates a type III functional response (Juliano 2001). After this step, the next phase involved estimating the functional response parameters. Roger's "random predator equation" (Royama 1971; Rogers 1972) was utilized to evaluate the handling time (T_h) and attack rate (a) coefficients associated with the type II functional response. The model is as follows:

$$N_a = N_0[1 - exp\big(a(T_hN_a - T)\big)] \text{ (Equation 2)}$$

Where:

N_a is the number of prey consumed; N_0 is the initial number of prey; T is the total time available for the predator to search during the experiment (24

h); a is the attack rate (searching efficiency); T_h is the handling time of the prey by the predator; and P_t is the number of predators (Rogers 1972). When the logistic regression analysis indicated that our data generally conformed to a type III functional response, the following equation was substituted for the attack rate (a) in Equation 3:

$$a = \frac{d + bN_0}{1 + cN_0} \quad \text{(Equation 3)}$$

When d and c are not significantly different from 0, this gives a = bN0, which can be inserted into Equation (2). This yields the following equation (Hassell 1978):

$$N_a = N_0[1 - exp(-bTN_0|1 + bT_hN_0^2)] \quad \text{(Equation 4)}$$

The notations of b, c and d are positive constants. Data analysis was performed using the Statistical Analysis System (SAS, version 9.1).

Results

Estimating functional response

The experiments showed that the functional response type of N. californicus changed across temperatures. Based on the logistic regression results, at temperatures from 10 to 25 °C, the linear coefficient of Equation 1 for this predatory mite was negative, indicating a type II functional response. However, at 30, 32.5, and 35 °C, logistic regression showed that the proportion of prey consumed was positively density-dependent, indicating a type III response ($P_1 > 0$) (Table 1). Figure 1 demonstrates the functional response of *N. californicus* to varying prey densities and temperatures. These findings provide strong evidence that temperature affects the foraging behavior of *N. californicus*. The outcomes of Roger's type III model indicate a significant increase in the attack coefficient (b) from 10 to 25 °C, while the values for attack rate (a) significantly increased from 30 to 35 °C, as estimated by Royama-Roger's type II. Another functional response parameter, handling time, decreased with increasing temperature from 15 to 30 °C. However, handling time differed significantly only at 25 and 30 °C compared with other temperatures. This parameter reached a minimum level at 30 °C (0.9076 h) (Table 2). Likewise, the estimated maximum predation rate (T/T_h) ranged from 21.42 (prey/day) at 15 °C to 26.44 (prey/day) at 30 °C.

Discussion

Environmental factors, specifically temperature, could affect the predation behavior of arthropod predators. Our findings clearly demonstrated the significant impact of temperature on the functional response of *N. californicus*. The predation by this predator on larvae and protonymphs of *T. urticae* exhibited a type III functional response at temperatures of 10, 15, 20, and 25 °C, while a type II functional response was observed at higher temperatures of 30, 32.5, and 35 °C. The Type III responses at lower temperatures suggest that prey capture was poor under these conditions, when prey populations were low. Hassell (1978) found that predators giving up searching at low prey densities can lead to a Type III functional response in many instances involving a single prey type. Although in the research done by Ahn *et al*. (2010) at temperatures of 15, 20, 25, 30, and 35 °C and Gotoh *et al*. (2004) at temperatures of 20, 25, and 30 °C, the functional response of *N. californicus* was a type II; however, other factors could also affect this behavioral attribute such as the type of host plant (Broufas and Koveos 2001; Madadi *et al., 2*007; Merlin *et al., 2*022; Azadi-Qoort *et al., 2*025), the age of the predator (Fathipour *et al., 2*017; Dalir *et al., 2*021), the species of prey, as well as their size and characteristics (Hassell 1978; Fan and Petitt 1994; Shirdel *et al*., 2004). We also observed a change in the type of functional response in response to temperature variations in *A. swirskii*. The functional response of *A. swirskii*, similar to the mite studied in our research, was type III at the lower temperature (25 °C) and type II at higher temperatures (30 and 35 °C) (Afshar and Latifi 2017). Additional studies on other phytoseiids have shown that most of them displayed a type II functional response across all tested temperatures, including *Neoseiulus womersleyi* (Schicha) and *N. longispinosus* (Evans) (Sugawara *et al., 2*018), *N. barkeri* (Jafari *et al., 2*012), and *Phytoseius plumifer* (Canestrini & Fanzago) (Kouhjani Gorji *et al., 2*009).

Table 1 Maximum likelihood estimates from logistic regressions of the proportion of *Tetranychus urticae* consumed by *Neoseiulus californicus* female adult as a function of initial prey density at different temperatures.

Temperatures (°C)	Parameters	Estimates (± SE)	□^{2}	*P*
	P_0	-0.3330 ± 0.2150	2.40	0.1215
	P_1	0.0652 ± 0.0169	14.89	0.0001
10	P_2	-0.0017 ± 0.0003	26.51	< 0.0001
	P_3	8.556E^{-6} ± 1.634E^{-6}	27.42	< 0.0001
	P_0	0.396 ± 0.2210	3.21	0.0731
	P_1	0.0300 ± 0.0172	3.07	0.0800
15	P_2	-0.0012 ± 0.0003	12.43	0.0004
	P_3	6.299E^{-6} ± 1.642E^{-6}	14.71	0.0001
	P_0	0.3722 ± 0.2270	2.69	0.1010
	P_1	0.0363 ± 0.0175	4.28	0.0386
20	P_2	-0.0013 ± 0.0003	14.60	0.0001
	P_3	6.871E^{-6} ± 1.667E^{-6}	16.99	< 0.0001
	P_0	1.0171 ± 0.2442	17.35	< 0.0001
	P_1	0.0058 ± 0.0184	0.10	0.7542
25	P_2	-0.0008 ± 0.0003	5.29	0.0214
	P_3	4.752E^{-6} ± 1.725E^{-6}	7.59	0.0059
	P_0	1.5416 ± 0.2673	33.27	< 0.0001
	P_1	-0.0227 ± 0.0196	1.34	0.2473
30	P_2	-0.0004 ± 0.0004	0.97	0.3250
	P_3	2.782E^{-6} ± 1.799E^{-6}	2.39	0.1220
	P_0	1.4378 ± 0.2636	29.75	< 0.0001
	P_1	-0.0118 ± 0.0197	0.35	0.5513
32.5	P_2	-0.0006 ± 0.0004	2.45	0.1176
	P_3	3.825E^{-6} ± 1.83E^{-6}	4.37	0.0366
	P_0	1.7253 ± 0.2823	37.35	< 0.0001
	P_1	-0.0196 ± 0.0205	0.91	0.3398
35	P_2	-0.0005 ± 0.0004	1.90 3.94	0.1677
	P_3	3.738E^{-6} ± 1.884E^{-6}		0.0472

Table 2 Estimates (± SE) of instantaneous attack rate (*a*) and handling time (T_h) of *Neoseiulus californicus* on *Tetranychus urticae* at different temperatures.

Temperatures (°C)	$^b a$, $^c b$ (h^{-1})	Type	$^a T_h$ (h)	$^d T/T_h$ (prey/ day)	R^2
10	0.0048 ± 0.000 (0.0037-0.0060)	Ⅲ	1.1198 ± 0.0245 (1.0711-1.1685)	21.43	0.98
15	0.0067 ± 0.0008 (0.0051-0.0084)	Ⅲ	1.1204 ± 0.0233 (1.0741-1.1668)	21.42	0.98
20	0.0068 ± 0.0008 (0.0053-0.0083)	Ⅲ	1.0957 ± 0.0205 (1.0549-1.1364)	21.90	0.98
25	0.0078 ± 0.0010 (0.0058-0.0097)	Ⅲ	1.0083 ± 0.0199 (0.9686-1.0480)	23.80	0.98
30	0.1280 ± 0.0150 (0.0981-0.1579)	Ⅱ	0.9076 ± 0.0246 (0.8587-0.9566)	26.44	0.98
32.5	0.1736 ± 0.0307 (0.1124-0.2347)	Ⅱ	1.0133 ± 0.0305 (0.9525-1.0740)	23.68	0.98
35	0.2329 ± 0.0507 (0.1321-0.3338)	Ⅱ	1.0383 ± 0.0309 (0.9768-1.0999)	23.11	0.98

*The values in parentheses represent 95% confidence intervals. $^a T_h$, handling time; $^b a$, attack rate; $^c b$, attack coefficient; $^d T/Th$, maximum predation rate.

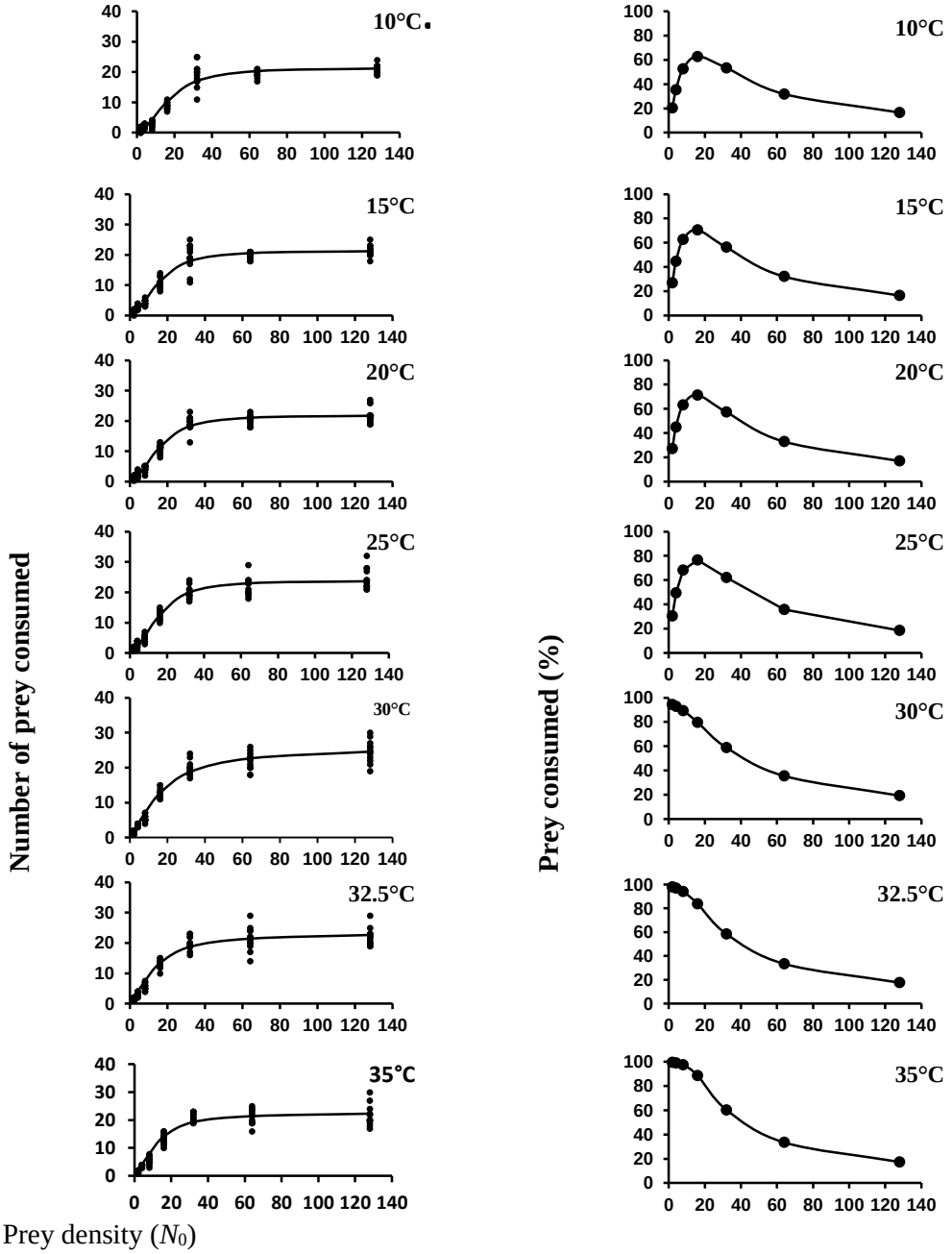


Figure 1 Number and percentage of *Tetranychus urticae* consumed by *Neoseiulus californicus* at different temperatures.

In addition to functional response type, temperature also affects functional response parameters such as handling time and attack rate. An extended model can account for differences in functional response to temperature by showing how temperature affects both handling time and attack rate (Ding-Xu *et al*., 2007). Handling time reflects the consumption rate and predator effectiveness, as it accounts for the total time invested in capturing, killing, and digesting prey (Veeravel and Baskaran, 1997). As noted in the results, handling time at 30 °C was

significantly lower than at other temperatures. At low temperatures, predators tend to spend more time on non-searching activities (*e.g.,* resting) (Ding-Xu *et al., 2*007). This pattern supports an increase in T_h at lower temperatures. However, the increase in this parameter at higher temperatures may be due to reduced metabolic activity through catabolism (Davis *et al., 2*006).

This decreasing-then-increasing trend in handling time was also observed in *N. womersleyi* and *P. persimilis* (> 30 °C in Sabelis and van der Meer, 1986; Sugawara *et al., 2*018). The results indicate that handling time significantly influences the performance efficiency of a predatory mite. In the present study, the highest maximum predation rate (T/T_h) was 26.44 prey per female at 30 °C. Although this rate is lower than that reported for *N. californicus* by Gotoh *et al*. (2004), which averaged 48.54 eggs per female per day, it is still a significant finding.

Additionally, we observed that the number of attacks increases with prey density, reaching a maximum attack rate at each experimental temperature. The functional response shows a type III at temperatures ranging from 10 to 25 °C. The attack coefficients (*b*) were low but positive. Our results show a clear linear increase in the number of consumed prey with prey density up to an inflection point, along with a corresponding increase in this coefficient with rising temperature. The observed trend in attack rate (*a*) further supports these findings. These results are consistent with previous studies by Gotoh *et al*. (2004) (at temperatures of 20, 25, and 30 °C) and Ahn *et al*. (2010) (at temperatures ranging from 15 to 35 °C). Overall, our research provides compelling evidence of the correlation between prey density, temperature, and predator behavior. Other predators such as *A. swiriskii* (Afshar and Latifi 2017) and *P. plumifer* (Kouhjani Gorji *et al., 2*009) exhibited an increased attack rate as temperatures rose.

The predator effectively managed T. urticae in the early growing season, as shown by the elevated predation rate at 30 °C, which declined at 32.5 °C and 35 °C. This aligns with Jafari et al. (2012), who found that predation by N. barkeri peaked at 35 °C before decreasing at 37 °C. Ganjisaffar *et al*. (2011) demonstrated that the prey consumption of *Typhlodromus bagdasarjani* (Wainstein & Arutunjan) follows a U-shaped curve with temperature, increasing from 15 to 25 °C, decreasing at 30 °C, and increasing again at 35 °C. Likewise, Kouhjani Gorji *et al*. (2009) noted a rise in the consumption rate of *P. plumifer* for the nymphal stages of *T. urticae* as the temperature increased from 15 to 35 °C. A similar pattern was also seen in *A. swiriskii* (Afshar and Latifi 2017).

Various studies highlight that temperature significantly influences prey consumption by predators. Other factors, such as predator species, host plants, prey life stages in the experimental arena, photoperiod, and humidity, can also affect predator feeding (Fernando and Hassell, 1980). *Neoseiulus californicus* is capable of controlling *T. urticae* and surviving at temperatures above 30 ℃, but performs better at lower temperatures. The low mortality rate observed in the temperature range of 20 to 30 °C supports this claim (Sedaghat *et al*., 2025). Therefore, *N. californicus* can be effectively integrated with other biocontrol agents to achieve optimal results in biological control programs. Nevertheless, while these controlled laboratory studies offer valuable insights into predator-prey dynamics, data on the functional response of *N. californicus* to *T. urticae* at various temperatures could be used to develop a model for an expert system. However, more studies are needed on other factors affecting the functional response and predation rate, including host plant traits, host patchiness, prey preference, and competition (Pervez 2005). It is also essential to investigate spatial complexity, the influence of other predators (Kareiva 1990), and the large search field (Murdoch, 1973; O'Neil 1989; Wiedenmann and O'Neil 1991) that dominates field conditions.

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Statement of Conflicting Interests
The authors state that there is no conflict of interest.

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واکنش تابعی وابسته به دما در کنه شکارگر (Acari: Phytoseiidae) *Neoseiulus californicus* روی کنه تارتن دو لکه‌ای (Acari: Tetranychidae) *Tetranychus urticae*

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چکیده: بررسی واکنش تابعی دشمنان طبیعی در دماهای مختلف برای ارزیابی کارایی آن‌ها در برنامه‌های مهارزیستی اهمیت زیادی دارد. از این‌رو، در این پژوهش واکنش تابعی کنه شکارگر *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) در تغذیه از لاروها و پروتونمف‌های کنه تارتن دولکه‌ای *Tetranychus urticae* Koch (Acari: Tetranychid) در هفت دمای ثابت شامل ۱۰، ۱۵، ۲۰، ۲۵، ۳۰، ۳۲/۵ و ۱ ± ۳۵ درجه سلسیوس بررسی شد. در هر دما، آزمایش‌ها در هفت تراکم طعمه شامل ۲، ۴، ۸، ۱۶، ۳۲، ۶۴ و ۱۲۸ لارو و پروتونمف انجام گرفت. نتایج حاصل از رگرسیون لجستیک نشان داد که در دماهای ۱۰، ۱۵، ۲۰ و ۲۵ درجه سلسیوس، واکنش تابعی از نوع سوم (Type III) بود، درحالی‌که در سایر دماهای مورد بررسی، واکنش تابعی از نوع دوم (Type II) مشاهده شد. نرخ حمله (*a*) و ضریب حمله (*b*) با افزایش دما افزایش یافتند؛ به‌طوری‌که بیشترین مقدار ضریب حمله ($b = 0.00777\ h^{-1}$) در دمای ۲۵ درجه سلسیوس و بیشترین نرخ حمله ($a = 0.2329\ h^{-1}$) در دمای ۳۵ درجه سلسیوس برآورد شد. هم‌چنین، بیشترین نرخ شکارگری طی ۲۴ ساعت و کوتاه‌ترین زمان دستیابی به طعمه (T_h) در دمای ۳۰ درجه سلسیوس ثبت شد. تراکم طعمه و دما تأثیر معنی‌داری بر میزان شکار *N. californicus* روی *T. urticae* داشتند؛ با این‌حال، اثر متقابل بین دما و تراکم طعمه معنی‌دار نبود. در تمامی دماهای مورد بررسی، با افزایش تراکم طعمه، میزان مصرف نیز افزایش یافت. در بالاترین تراکم طعمه (۱۲۸ فرد)، بیشترین میزان مصرف در دمای ۳۰ درجه سلسیوس مشاهده شد. درمجموع، بررسی واکنش تابعی و ظرفیت شکارگری *N. californicus* در تغذیه از لاروها و پروتونمف‌های *T. urticae* نشان داد که این کنه شکارگر می‌تواند، به‌ویژه در دماهای بالاتر از ۲۵ درجه سلسیوس، به‌عنوان یک عامل مؤثر در مهار زیستی این آفت مورد استفاده قرار گیرد.

واژگان کلیدی: نرخ حمله، نرخ شکارگری، زمان دستیابی، واکنش تابعی، *Tetranychus urticae*