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Article

The impact of food stress-induced learning on compensatory behaviors in predatory mites *Phytoseiulus persimilis* and *Neoseiulus californicus* (Acari: Phytoseiidae)

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ABSTRACT
Learning and early-life experiences are crucial in enhancing predatory behavior and resource utilization among predators, increasing their ability to adapt to fluctuating environmental conditions. Foraging predators exposed to food-related stress often develop compensatory behaviors that support their survival and reproductive success in resource-scarce environments. This study examines the effects of food stress during nymphal and adult stages on the predation behavior and fecundity of two predatory mites, *Neoseiulus californicus* (McGregor) and *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) feeding on two-spotted spider mite *Tetranychus urticae* Koch. In the first experiment, mites experienced food stress during the nymphal stage, resulting in significantly higher predation rates but lower egg production in adulthood compared to controls. In the second experiment, mites faced 24 hours of food stress only in adulthood, leading to increased predation and reduced egg production compared to controls. In the third experiment, *N. californicus* reared solely on pollen from egg to adulthood exhibited enhanced predation and decreased egg production as adults. These findings highlight the adaptive potential of food-stress-induced compensatory behaviors, including enhanced predation efficiency and reduced fecundity, which act as survival strategies under resource constraints. The study underscores the role of mechanisms such as learning and energy optimization in facilitating these responses. Moreover, these adaptive behaviors present valuable opportunities for Integrated Pest Management (IPM) programs by enhancing the performance of biological control agents under variable environmental conditions.

KEYWORDS: Compensatory behavior, food stress, flexibility, learning, predatory mite.

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INTRODUCION

The behavioral evolution brought about by prey experience, generally life-stage and phase-specific dependent in many organisms, mostly happens at the early life stages in which the organisms are susceptible to environmental motivations (Domínguez 2014; Stamps and Krishnan 2017; Schausberger *et al*. 2018). Natural selection forms the capability to learn, but its phenotypic declaration is strongly context-dependent (Reichert *et al*. 2017). Also, learning as a broad phenomenon applies by foraging predators in order to promote behaviors such as prey searching, diagnosis, and capture

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(Dukas 2008; Stephens and Dunlap 2017; Schausberger *et al.* 2020). Some studies have noted that diet-related situations i.e. access, limitation, and the nutritional mixture of food, could strongly affect the expression level of learning in *Drosophila melanogaster* Meigen (Xia *et al.* 1997; Kawecki 2010). This knowledge has the potential to revolutionize pest control practices, making them more adaptable to environmental variability.

Long-term adaptations, through natural selection, may direct to a match between organisms and their environment (Smith and Winterhalder 2017). On the other hand, short-term changes in environmental factors can interrupt this accordance and negatively affect the survival and fitness of an organism (Nussey *et al.* 2007; Whitman and Agrawal 2009; Le Hesran *et al.* 2020). Early developmental stages such as eggs and larvae are mostly considered vulnerable to environmental tensions, because of their restricted dispersal capability and their small size (Schausberger 1998; Montserrat *et al.* 2007; Walzer *et al.* 2007; Ferrero *et al.* 2010; Potter and Woods 2012; Torres-Campos *et al.* 2016; Le Hesran *et al.* 2020), so that the path through which females ensure the survivorship of their progeny is an indispensable question when studying behavioral plasticity associated with learning. This highlights the importance of investigating early-life experiences and environmental stressors to develop effective biological control agents that are more resilient to environmental fluctuations.

The significance of learning and early life hunting experiences can have a profound impact on the biological control of pests, especially in predatory species whose foraging behavior is strategically adapted to environmental conditions (Fox *et al.* 2001; Lo Pinto *et al.* 2004). Early experiences, particularly those involving food stress, often enhance hunting skills and the capacity for resource storage, which, in turn, improves the survival rates and success of predators in fluctuating and resource-limited environments (Hassell 2000; Schausberger *et al.* 2020). Furthermore, predators' ability to learn and increase predation rates optimizes their foraging efforts, enhancing their effectiveness as biological control agents (Abrams and Holt 2002; Dukas 2008). This capability is particularly crucial when facing periods of food scarcity, as predators can draw on previous experiences to adopt compensatory strategies in resource use and conservation (Stephens and Krebs 1986; Whitman and Agrawal 2009). Understanding these mechanisms is critical for improving the application of behavioral adaptations in Integrated Pest Management (IPM) programs, where learning and adaptive foraging behaviors can significantly enhance pest suppression.

The predatory mite *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) is known as an important biocontrol agent that feeds on herbivorous mite two-spotted spider mite *Tetranychus urticae* Koch. It belongs to the Type II selective predators of tetranychid mites (McMurtry *et al.* 2013; Farazmand *et al.* 2012). It not only has the competency of killing tetranychid species, but also the ability to kill small insects and can even survive on other non-prey food sources like pollen (Swirski *et al.* 1970; McMurtry *et al.* 2013). The phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) is considered a basic bio-control agent that is generally recommended for the control of tetranychid mites particularly due to its specialization as a Type II predator (Abad-Moyano *et al.* 2010; Weintraub and Palevsky 2008). This species feeds solely on all life stages of web-nest-producing spider mites (McMurtry *et al.* 2013).

Predator learning ability changes during its lifetime. Different stages might differ in attack latency and other behavioral and physiological aspects (Christiansen *et al.* 2016). Here, we have scrutinized the factors influencing for the learning ability in natural prey and pollen-reared line of these predatory mites. Several studies have considered the fundamental effects of diet on expressions in the predatory mites. Previous studies have reported that the early experiences of odors related to foraging activities would lead to some significant and continuous behavioral changes in predatory mites *N. californicus*, *P. persimilis*, and *Amblyseius swirskii* Athias-Henriot (Rahmani *et al.* 2009; Christiansen *et al.* 2016; Seiter and Schausberger 2016; Christiansen and Schausberger 2017).

Given the importance of this issue, this study aims to shed light on the behavioral flexibility of predatory mites in response to food stress. To date, little attention has been given to exploring behavioral adaptations and learning mechanisms in predatory mites under such conditions. The results of this research aim to provide a deeper understanding of the behavioral adaptations and learning mechanisms in predatory mites, contributing to optimizing pest control methods and enhancing their efficiency within agricultural systems, while also facilitating the development of more effective Integrated Pest Management (IPM) strategies and sustainable agricultural practices.

MATERIALS AND METHODS

*Two-spotted spider mite (*T. urticae*)*

Common bean plants [*Phaseolus vulgaris* L. (Fabaceae) var. Red Alamouti] were grown in plastic pots in a greenhouse (soil: perlite; 50:50%) under controlled conditions (25 ± 5 °C, 16L:8D photoperiod, 65 ± 5% RH) at the Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran. Plants were irrigated daily with tap water and fertilized every other day with an NPK (20 × 20 × 20) solution. Two-spotted spider mites (*T. urticae*, green form; food source for the predatory mites) were sourced from an existing colony maintained in the acarology greenhouse. To rear them, infested bean leaves were transferred to healthy plants, where the mites quickly established and multiplied. Fresh bean plants were added to the rearing system regularly to maintain the population.

Predatory mites

The predatory mites, *P. persimilis* and *N. californicus* (maintained in the Acarology laboratory at the University of Tehran), were reared on masses of detached bean leaves, infested with *T. urticae*, placed upside down on a plastic sheet on a water-saturated sponge. The plastic sheet was surrounded by napkin tapes which were placed into the water to allow the predatory mites to drink. Fresh *T. urticae*-infested leaves and fresh corn pollen (*Zea mays* L.) were added to the rearing system and the old predator-free leaves were removed regularly (Overmeer 1985). The cultures were kept in growth chambers under controlled conditions (25 ± 1 °C, 16L:8D photoperiod, 65 ± 5% RH) in the Acarology laboratory at Jalal Afshar Zoological Museum, Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran.

Pollen collection

Pollen of maize was gathered from *Zea mays* L. (maize) plants (Tehran, Iran; 35° 48' 25.3" N, 50° 59' 38.3" E) from spring to summer. Pollen was oven-dried (at 37 °C for 48 h), and then was refrigerated at 4 °C for a maximum of three weeks usage. The inclusion of pollen in this study pertains specifically to *N. californicus*, as this species can subsist solely on pollen when prey is unavailable due to its high nutritional value. However, pollen-fed *N. californicus* demonstrates reduced efficiency as a predator compared to its performance when feeding on *T. urticae*.

Experimental arena

The experimental arena was constructed according to the Abou-Setta and Childers method (Abou-Setta and Childers 1987). A hole (1 cm in diameter) was made at the center of each plastic Petri dishe (9 cm in diameter). The first Petri dish was sealed using glue to the other one, which was used for supplying water. Two pores (2 cm in diameter) were created in the upper part of the second Petri dish to fill it with water. A wick prepared from filter paper was passed from the central hole to the second Petri dish. The wick was provided with water to keep the leaves fresh in the upper Petri dish. A thin layer of moist cotton was placed at the bottom and was covered with filter paper to prevent the leaf from drying out. All the leaves were placed on the filter paper in the Petri dishes. The experimental arena was covered with a ventilated lid.

Pre-testing and preparation of predatory mites for experiments

To determine the prey density required to induce food stress, preliminary experiments were conducted using different prey densities (2–15 *T. urticae* nymphs per leaf). Based on these pre-test results, a prey density of three spider mites per leaf was considered insufficient, while 10 spider mites per leaf was considered sufficient as the control treatment. These prey densities were employed in subsequent experiments. The experimental setup consisted of a bean leaf disk put upside down on a layer of water-saturated cotton. An equal number of same-aged male and female predators (either *P. persimilis* or *N. californicus*) were transferred onto leaf discs using a fine soft pointed brush. Five Petri dishes were considered for each treatment (control or food-stressed) and kept in growth chamber under controlled conditions (25 ± 1 °C, 16L:8D photoperiod, 65 ± 5% RH). After 24 h, the adults were removed and only eggs remained. The predators were reared for three generations using the specific daily diet in the forms of either sufficient or insufficient food. The eggs related to the third generation were collected daily and transferred individually to the new experimental arenas, containing a part of bean leaf [2 × 2 cm] placed upside down on a dense foam pad [3 × 3 cm] and a moist tissue cotton wool wrapped around the edges of leaf discs to prevent the mites from escaping. The larvae hatched from these eggs (reared on either sufficient or insufficient diets) were used in the next experiment.

Food stress during the predator protonymph stage

To investigate the impact of food stress during the immature stages on adult predator efficacy, larvae hatched from eggs obtained in the previous experiment (including both control and food-stressed treatments) were reared on a diet of 10 spider mites per day until reaching the protonymph stage (although *P. persimilis* larvae do not feed, and *N. californicus* larvae feed very little). Food stress was applied upon reaching the protonymph stage, during which individuals in the food-stressed treatment were provided with a reduced diet of three spider mites for 24 hours. After that, both treatments were fed 10 spider mites daily, continuing through the deutonymph stage and into adulthood. Once 48h-aged adult mites emerged, 40 adult mites (males or females) from each treatment were individually transferred to 40 Petri dishes maintained under identical conditions as the previous experiment. To assess maximum daily predation rates, a large number of spider mites were added to each Petri dish. For enhanced precision, prey age was standardized: 20 Petri dishes contained same-aged protonymph spider mites, while the remaining 20 received same-aged deutonymphs. A single adult male mite was subsequently added to each dish containing a female for mating. Adult predation rates were recorded at 3, 6, and 24 hours post-adult emergence, followed by predator oviposition rate assessments at 24 and 48 hours.

Food stress during the early adult stage of predators

This experiment was performed on predators that had no food stress during the immature stages (eggs to adults). One-day-old female predators of the same age were individually transferred to Petri dishes containing either 3 or 10 spider mites as insufficient and sufficient food respectively. After 24h, the 48h-aged female predators were individually transferred to new Petri dishes containing a large number of same-aged spider mites (protonymph or deutonymph). A single adult male was introduced to each dish containing female. The predator oviposition rate was recorded 24 and 48 hours later. Moreover, adult predation rates were recorded at 3, 6 and 24 hours post-adulthood. The experiment was performed in 20 replicates.

Food stress from egg to adult (on N. californicus*)*

This experiment investigated the influence of exclusive pollen-based diet, with no access to spider mites, throughout the entire life cycle of *N. californicus* (egg to adult) on subsequent adult predation and oviposition rates. To obtain same-aged eggs, gravid female predators were transferred to rearing units comprising a detached bean leaf (2 × 2 cm) placed upside down on a dense foam pad

(3 × 3 cm) with maize pollen provided. A consistent supply of fresh pollen was provided daily until the emergence of adults (females and males, 5–7 days). Upon adult emergence, pollen was provided only on the first day and subsequently eliminated from the diet, initiating the experimental phase. Forty 48h-aged adults (males or females) were individually placed in 40 Petri dishes. Twenty of these dishes contained a sufficient number of spider mite protonymphs, while the remaining 20 were populated with spider mite deutonymphs. An adult male was also transferred into each Petri dish containing one 48h-aged female. Predation rates of adult predators were assessed at 3, 6, and 24 hours post-introduction to experimental arenas. Predator oviposition was also recorded at 24 and 48 hours post-experiment initiation.

Table 1. Summary of experimental steps: Predator's life stages and food diet of each stage.

The hunger-stressed stage	**N**	**Diet of predatory mite life stages (The number of *T. urticae* provided to each stage prior to or during the experiment)**				
		Larva	**Proto** [a]	**Deuto** [b]	**24h adult**	**48h adult**
Control	20	10	10	10	10	Exp [c] (20 proto)
	20	10	10	10	10	Exp (20 deuto)
Protonymph	20	10	3	10	10	Exp (20 proto)
	20	10	3	10	10	Exp (20 deuto)
Early adult stage	20	10	10	10	3	Exp (20 proto)
	20	10	10	10	3	Exp (20 deuto)
Egg to adult [d]	20	Pollen	Pollen	Pollen	Pollen	Exp (20 proto)
	20	Pollen	Pollen	Pollen	Pollen	Exp (20 deuto)

[a] Protonymphs, [b] Deutonymphs, [c] Experiment, [d] only for *N. californicus*

Data analysis

The analysis of variance (ANOVA) was performed to identify significant differences in predation and oviposition rates. A one-way ANOVA was used to analyze the effects of food stress on predation and oviposition rates across different treatments. Each treatment consisted of 20 replicates. Prior to performing ANOVA, the Shapiro-Wilk test was applied to assess the normality of the data distribution. For experiments involving two treatments, the Student's t-test was employed to compare means. When a significant difference was detected ($P < 0.05$), Tukey's HSD test (for ANOVA) or pairwise comparisons (for t-tests) were employed for post-hoc. All analyses were performed using SAS software (version 9.4; SAS Institute 2013).

RESULTS

The effect of food stress during the nymphal and early adult stages on the predation rate of adult predators

The results in Table 2 show that the predation rates of both *P. persimilis* and *N. californicus* were consistently higher in individuals exposed to food stress during their nymphal or early adult stages compared to those reared under non-stressed (control) conditions. In *P. persimilis*, this trend was observed across all time intervals (3, 6, and 24 hours post-experiment initiation) and for both prey stages (protonymphs and deutonymphs), with stressed individuals consistently preying on significantly more *T. urticae* than the controls. Similarly, for *N. californicus*, food-stressed individuals also exhibited higher predation rates compared to the controls across all treatments and time intervals. However, a notable exception was observed in the 24-hour treatment when feeding on deutonymphs: no significant difference was detected between the controls and individuals that experienced food stress during the nymphal stage. This exception suggests that, under specific conditions, the compensatory predation behavior in *N. californicus* may be less pronounced or influenced by other factors, particularly when deutonymphs are the primary prey.

Table 2. Effect of nymphal and early adult food stress on predation rates of adult female *Phytoseiulus persimilis* and *Neoseiulus californicus* feeding on *Tetranychus urticae*.

Sexuality		**Predation rates (± SE) of *P. persimilis***			**Predation rates (± SE) of *N. californicus***		
		Control	**Nymphal stress**	**Early adult stress**	**Control**	**Nymphal stress**	**Early adult stress**
Prey Stage	**Male**						
Protonymph	3 hours	2.46 ± 0.15a	3.26 ± 0.29b	3.59 ± 0.30b	2.53 ± 0.18a	3.61 ± 0.24b	3.46 ± 0.33b
	6 hours	5.81 ± 0.23a	7.15 ± 0.33b	8.02 ± 0.28b	4.73 ± 0.22a	7.13 ± 0.26b	7.46 ± 0.32b
	24 hours	11.21 ± 0.35a	13.02 ± 0.3b	12.91 ± 0.45b	9.12 ± 0.24a	12.26 ± 0.4b	12.13 ± 0.33b
	Female						
	3 hours	4.13 ± 0.20a	6.01 ± 0.33b	7.07 ± 0.22b	2.86 ± 0.22a	5.61 ± 0.2b	6.01 ± 0.36b
	6 hours	8.53 ± 0.24a	11.07 ± 0.4b	11.95 ± 0.38b	7.82 ± 0.23a	11.22 ± 0.25b	12.26 ± 0.29b
	24 hours	14.53 ± 0.36a	17.94 ± 0.3b	17.97 ± 0.17b	12.46 ± 0.22a	17.20 ± 0.34b	18.13 ± 0.24b
Deutonymph	**Male**						
	3 hours	1.86 ± 0.18a	4.06 ± 0.19b	4.06 ± 0.23b	2.01 ± 0.18a	3.00 ± 0.21b	3.31 ± 0.32b
	6 hours	4.13 ± 0.22a	7.95 ± 0.31b	6.93 ± 0.30b	4.06 ± 0.19a	6.41 ± 0.33b	7.26 ± 0.38b
	24 hours	8.13 ± 0.31a	13.96 ± 0.39c	9.93 ± 0.22b	8.81 ± 0.16a	10.13 ± 0.26b	11.13 ± 0.26b
	Female						
	3 hours	2.21 ± 0.23a	3.94 ± 0.27b	3.62 ± 0.22b	2.22 ± 0.16a	3.53 ± 0.20b	4.06 ± 0.19b
	6 hours	4.86 ± 0.18a	8.48 ± 0.24b	7.94 ± 0.30b	5.23 ± 0.23a	7.04 ± 0.31b	8.21 ± 0.31b
	24 hours	10.21 ± 0.28a	14.81 ± 0.44c	12.94 ± 0.31b	10.56 ± 0.24a	10.53 ± 0.32a	13.26 ± 0.37b

Means within a row followed by the same letter for each species are not significantly different according to Tukey's HSD test at the 95% confidence level.

Table 3. Effect of food stress (pollen diet) during the entire immature stages (egg to adult) on the adult predation rate of *N. californicus*.

Sexuality		**Predation rate (± SE) of *N. californicus***	
		Control	**Egg to adult stress**
Prey Stage	**Male**		
Protonymph	3 hours	2.53 ± 0.18a	3.21 ± 0.26b
	6 hours	4.73 ± 0.22a	6.62 ± 0.36b
	24 hours	9.00 ± 0.24a	10.46 ± 0.40b
	Female		
	3 hours	2.86 ± 0.22a	4.86 ± 0.22b
	6 hours	7.81 ± 0.23a	10.13 ± 0.15b
	24 hours	12.46 ± 0.22a	15.26 ± 0.25b
Deutonymph	**Male**		
	3 hours	2.00 ± 0.18a	3.00 ± 0.21b
	6 hours	4.06 ± 0.19a	6.41 ± 0.33b
	24 hours	8.81 ± 0.16a	10.13 ± 0.26b
	Female		
	3 hours	2.22 ± 0.16a	3.53 ± 0.20b
	6 hours	5.21 ± 0.23a	7.04 ± 0.31b
	24 hours	10.50 ± 0.24a	10.58 ± 0.32a

Means within a row followed by the same letter for each species are not significantly different at the 95% confidence level (t-test).

The effect of food stress during the entire immature stages (egg to adult) on the adult predation rate of N. californicus

According to the results in Table 3, when *N. californicus* experienced stress by feeding on pollen, both male and female predation rates on *T. urticae* protonymphs were significantly higher than the control at all observation intervals (3, 6, and 24 hours). The predation rate of male *N. californicus* on *T. urticae* protonymphs after 24 hours (10.46 per individual) were significantly higher than the control (9.00 per individual). Similar results were observed for both male and female *N. californicus* feeding on *T. urticae* deutonymphs, but the predation rate of females did not differ significantly in comparison with control after 24 hours.

The effect of nymphal and early adult food stress on the oviposition rate of adult predatory mites

Based on our results in Table 4, the oviposition rates of *P. persimilis* females subjected to food stress during both nymphal and early adult stages did not significantly differ from controls at 24 hours post-mating. However, a significant reduction in oviposition rate was observed in females experiencing early adult food stress at the 48-hour post-mating interval. For *N. californicus*, females subjected to food stress during either the nymphal or early adult stages exhibited significantly lower oviposition rates compared to controls at both 24 and 48 hours post-mating, with greater reductions observed in those stressed stages.

Table 4. The effect of nymphal and early adult food stress on the average number of eggs (Mean ± SE) laid by *Phytoseiulus persimilis* and *Neoseiulus californicus* females.

Time	Number of eggs (± SE) laid by *P. persimilis*			Number of eggs (± SE) laid by *N. californicus*		
	Control	Nymphal stress	Early adult stress	Control	Nymphal stress	Early adult stress
24 hours	1.89 ± 0.09a	1.74 ± 0.11a	1.46 ± 0.12a	1.00 ± 0.07a	0.53 ± 0.09b	0.54 ± 0.12b
48 hours	4.00 ± 0.08a	3.86 ± 0.18a	3.53 ± 0.19b	2.08 ± 0.08a	0.95 ± 0.08b	0.86 ± 0.11b

The unit for egg counts is based on the average number of eggs laid per individual.

Means within a row followed by the same letter for each species are not significantly different according to Tukey's HSD test at the 95% confidence level.

The effect of food stress during the entire immature stages (egg to adult) on the oviposition rate of N. californicus

Table 5 illustrates a marked decrease in the fecundity of *N. californicus* females reared exclusively on a pollen-only diet during their immature stages compared to those reared on a diet including spider mites. At 24 and 48 hours post-mating, mean egg production in pollen-fed females (0.46 and 0.81 eggs per female, respectively) was significantly lower than the control group (1.0 and 2.08 eggs per female) and even dropped to less than half the control values. In the control treatment, females were reared on a diet that included spider mites, further underscoring the negative impact of a pollen-only diet.

Table 5. The effect of food stress (pollen-only diet) entire immature stages (egg to adult) on the average number of eggs (Mean ± SE) laid by *Neoseiulus californicus* females.

Time	Number of eggs (± SE) laid by *N. californicus*	
	Control	Egg to adult stress
24 hours	1.00 ± 0.07a	0.46 ± 0.03b
48 hours	2.08 ± 0.08a	0.81 ± 0.05b

The unit for egg counts is based on the average number of eggs laid per individual.

Means within a row followed by the same letter for each species are not significantly different at the 95% confidence level (t-test).

DISCUSSION

Learning is a dynamic process involving the acquisition, retention, and utilization of information, which results in behavioral adaptations over time (Alcock 2001; Dukas 2008). Among invertebrates, learning has been well-documented in predatory mites of the family Phytoseiidae, which inhabit plants and adapt their behaviors to varying environmental conditions (Schausberger 2007; Schausberger *et al*. 2010; Strodl and Schausberger 2012). Early developmental stages, particularly the larval and early protonymphal phases, are considered the most critical for learning, as they influence future foraging and reproductive strategies (Schausberger 2007; Christiansen *et al*. 2016). However, the link between food stress—particularly non-prey diets—and learning in phytoseiid mites remains insufficiently studied, with limited focus on how diet stress shapes compensatory behaviors through learning. Our findings provided new insights, indicating how diet stress influences adaptive predatory strategies and reproductive trade-offs in the predatory mites.

According to the results in Tables 2 and 3, when *N. californicus* and *P. persimilis* experienced food stress during the nymphal stage or early adulthood, they exhibited significantly higher predation rates compared to those not exposed to such stress (control). These findings suggest that predators with prior food stress may acquire a form of learning or adaptation to food scarcity, explaining the observed increase in predation rates. It appears that after experiencing food stress during immature stages or adulthood, these predators display compensatory behaviors, such as increased predation rates, as a strategy to offset potential future shortages. Only *N. californicus* nymphs subjected to food stress showed no significant difference from the control in feeding on two-spotted spider mite deutonymphs 24 hours post-adulthood. This lack of difference shows that *N. californicus* may possess more effective storage capabilities or metabolic adaptations during the nymphal stage, allowing them to partially mitigate the effects of food stress. Consequently, after reaching adulthood, the impact of this stress on their predatory behavior is reduced. Additionally, this species may exhibit behavioral plasticity that enables them to utilize resources more efficiently after food stress without an immediate increase in predatory behavior.

Similar studies on insects and predatory animals show that stressful conditions induce behavioral and physiological changes that support survival under adverse circumstances (Tian *et al*. 2020; Xu *et al*. 2024). The hypothesis that predators exhibit greater hunting tendencies after food stress can be explained by physiological and behavioral mechanisms as compensatory responses to scarcity. Animals experiencing past food shortages may inherently show higher predation tendencies to rebuild energy reserves and prepare for future shortages (Wang *et al*. 2019**)**. This aligns with the concept of "conditional learning in predators" where food stress leads to unconscious retention of the experience, resulting in compensatory predation increases when conditions normalize. Animals may develop a "nutritional memory" that ensures sufficient energy storage at optimal times. These findings align with those of Reichert *et al*. (2017), who showed that early experiences, including exposure to thrips during larval and protonymphal stages, and generational traits, influence the attack latency of adult *Amblyseius swirskii* Athias-Henriot females toward thrips larvae. Their study concluded that pre-laying diets shape feeding strategies, adapting offspring behavior to unpredictable food conditions and preserving learning abilities to enhance predation efficiency.

A plausible interpretation for the increased predation rate in *N. californicus,* fed only pollen, is that food stress, even without access to actual prey, may lead to learning or behavioral adjustment that enhance future predation efficiency. Although this predator did not encounter prey during immature stages, food limitation seems to prepare it mentally and behaviorally to exploit food resources more effectively in the future. Such conditions may activate adaptive responses, leading to stronger predatory behaviors when food becomes available. These compensatory and adaptive behaviors, indicate that a pollen-based diet can be an adequate trigger for eliciting such adaptive responses.

Investigations into food stress in predatory mites, with some differences in approach, have revealed notable adaptive responses. For instance, Tian *et al*. (2020) found that short-term starvation in *Pyemotes zhonghuajia* Yu, Zhang & He (Trombidiformes: Pyemotidae) enhanced predation efficiency by increasing movement and reducing the time to parasitize hosts, although prolonged starvation led to diminished performance. Similarly, Lemos *et al*. (2023) observed that while low-quality prey reduced survival and reproduction in *P. persimilis*, it supported short-term survival under food stress, reflecting the resilience of predators when faced with limited food availability. Xu *et al*. (2024) further highlighted the critical role of early-life nutrition in shaping life history traits, demonstrating that food stress during immature and early adult stages of *P. persimilis* had a more pronounced impact on reproductive traits than stress experienced later in life. Additionally, Barros-Bellanda and Zucoloto (2002) reported that short-term food stress in larvae of *Ascia monuste orseis* (Lep.: Pieridae) resulted in prolonged development, reduced survival, and fecundity, with compensatory feeding in later instars serving as an adaptive mechanism to counter early nutritional deprivation. Sheng *et al*. (2024) also found that starvation during developmental stages in *Amblyseius orientalis* Ehara (Acari: Phytoseiidae) extended adult lifespan but reduced reproductive output, suggesting a trade-off between survival and reproduction under food stress. Collectively, these studies reveal the nuanced effects of food deprivation across species and stages, many of which align with our findings that food stress during immature stages enhances compensatory behaviors and increases predation rates in predatory mites.

Based on Tables 4 and 5, the reduction in egg production among predators after food stress is logical, as oviposition requires adequate nutrition, and scarcity depletes energy reserves, acting as a survival mechanism (Walzer and Schausberger 2015). Plant-based food, compared to animal-derived food, often lacks nutrients essential for optimal nervous system function, such as B vitamins (especially B12), essential amino acids, Omega-3 fatty acids, and minerals like iron (Gómez-Pinilla 2008; Guesnet and Alessandri 2011; Kennedy 2016; Khanamani *et al*. 2017). These deficiencies may further limit energy availability and reproduction (Lundgren 2009), prioritizing survival over reproduction during nutritional stress, highlighting a resource allocation strategy to endure scarcity (Walzer and Schausberger 2015; Khanamani *et al*. 2017).

In a study by Al-Azzazy and Alhewairini (2024), *Phytoseius plumifer* Canestrini & Fanzago (Acari: Phytoseiidae) fed solely on plant-derived pollen exhibited significantly reduced oviposition rates and shorter lifespans compared to those fed on natural prey, *Oligonychus afrasiaticus* McGregor (Acari: Tetranychidae), emphasizing the importance of primary prey for reproductive performance. Similarly, Walzer and Schausberger (2015) found that severe food stress caused most females in generalist species like *Amblyseius andersoni* Chant (Acari: Phytoseiidae) to lay only one small egg or cease oviposition entirely. However, *P. persimilis* and *N. californicus*, more specialized for spider mite prey, continued oviposition under stress but at reduced rates. The findings highlight an adaptive strategy to conserve energy by reducing energetically costly female eggs, prioritizing survival under resource limitations. Park *et al*. (2011) examined the effects of diet on *Amblyseius swirskii* and found that individuals consuming tomato russet mites (*Aculops lycopersici* Tryon) had enhanced reproductive output and faster development compared to those fed on cattail pollen. This preference for mite prey led to higher egg production and a quicker life cycle, showing that russet mites optimize *A. swirskii*'s growth and reproduction. Similarly, Schausberger *et al*. (2018) investigated behavioral plasticity in *A. swirskii,* evaluating prey experiences from juvenile to adulthood with thrips and spider mites. Early-life prey experiences promoted learning, enabling faster attacks and prioritization of familiar prey, while adulthood experiences induced general physiological changes regardless of prey type. Faster attacks correlated with higher egg laying, emphasizing the adaptive effects of early-life experiences on feeding efficiency and reproduction, with adulthood effects remaining generalized and non-specific.

From a biological perspective, these predators are evolutionarily programmed to develop stress-induced behaviors that enhance adaptability to complex environments and ensure survival. This flexibility requires linking information processing to appropriate behavioral responses through an interaction of innate behaviors and accumulated life experiences (learning) (Wright *et al*. 2010). The evolution of learning and innate responses depends on their fitness costs and benefits, with natural selection indirectly shaping both via behavioral flexibility. The combination of innate plasticity and learning produces more adaptive outcomes than either alone (Mery and Burns 2010).

In conclusion, past experiences of food scarcity in predators lead to compensatory behavioral patterns, such as increased predation and reduced oviposition, which optimize energy use and resource storage. This highlights the role of environmental conditions in shaping survival-oriented behaviors in animals. The findings of this study have significant implications for the use of *N. californicus* and *P. persimilis* in integrated pest management (IPM) programs. Releasing pest-experienced predators into pest-infested areas could offer a substantial advantage in boosting predator population growth and ensuring effective pest control. This approach could be particularly valuable if pest-naive predators reared on artificial diets show limited developmental adaptability. This work underscores the importance of understanding predator behavioral adaptations to stress, as these insights can inform more resilient and sustainable pest management strategies. By employing pest-acclimated predators, IPM strategies can significantly increase predation rates, enhance pest control efficiency, and minimize dependence on chemical pesticides. Ultimately, these findings emphasize the critical role of understanding predator behavioral adaptations to food stress, offering valuable insights for developing more sustainable and resilient pest management approaches.

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تأثیر یادگیری ناشی از تنش غذایی بر رفتارهای جبرانی در کنه‌های شکارگر Phytoseiulus persimilis و Neoseiulus californicus (Acari: Phytoseiidae)

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چکیده

یادگیری و تجربیات اولیه نقش مهمی در بهبود کارایی شکارگری و بهره‌برداری از منابع در شکارگران ایفا می‌کنند و توانایی آن‌ها را برای سازگاری با شرایط محیطی متغیر افزایش می‌دهند. شکارگرانی که در معرض تنش غذایی قرار می‌گیرند، اغلب رفتارهای جبرانی را توسعه می‌دهند که زنده‌مانی آن‌ها را در محیط‌های با تراکم کم غذا تضمین کرده و موفقیت تولیدمثلی آن‌ها را افزایش می‌دهد. در این پژوهش اثرهای تنش غذایی در مراحل نابالغ و بالغ را بر رفتار شکارگری و میزان باروری دو گونه هرنای شکارگر *Neoseiulus californicus* (McGregor) و *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) بررسی شده است که از هرنای تارتن دولکه‌ای *Tetranychus urticae* Koch تغذیه می‌کنند. در آزمایش نخست، هرناها در مرحلهٔ پوره سن یکم تحت تنش غذایی قرار گرفتند که منجر به افزایش معنی‌دار میزان شکار در دوره بلوغ شد، اما میزان تخم‌گذاری آن‌ها در مقایسه با گروه شاهد کاهش یافت. در آزمایش دوم، هرناها بعد از بلوغ به مدت ۲۴ ساعت با تنش غذایی مواجه شدند که این شرایط نیز منجر به افزایش شکار و کاهش تخم‌گذاری در مقایسه با گروه شاهد شد. در آزمایش سوم، هرنای *N. californicus* که از مرحلهٔ تخم تا بلوغ فقط با گرده تغذیه شده بود، در دورۀ بلوغ افزایش رفتار شکارگری و کاهش تخم‌گذاری را نشان داد. این یافته‌ها بر توان بالقوه رفتارهای جبرانی ناشی از تنش غذایی تأکید دارند که شامل افزایش کارایی شکار و تنظیم الگوی باروری است، به‌گونه‌ای که کاهش تخم‌گذاری در کنار شکار مؤثرتر به حفظ منابع حیاتی و افزایش شانس زنده‌مانی در شرایط کمبود منابع کمک می‌کند. این نتایج نقش سازوکارهایی مانند یادگیری و بهینه‌سازی مصرف انرژی را در تسهیل این پاسخ‌ها برجسته می‌سازد. افزون بر این، چنین رفتارهای تطبیقی فرصت‌های ارزشمندی را برای برنامه‌های مدیریت تلفیقی آفات (IPM) فراهم می‌کند زیرا می‌توانند به بهبود عملکرد عوامل مهار زیستی در شرایط محیطی متفاوت کمک کنند.

کلمات کلیدی: رفتار جبرانی، تنش غذایی، انعطاف‌پذیری، یادگیری، هرنای شکارگر.

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