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Predator egg-induced non-consumptive effects suppress spider mite survival and reproductive performance

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Abstract

BACKGROUND: Predators suppress pest populations not only through direct consumption but also via non-consumptive effects (NCEs), in which prey perceive predation risk and alter behaviors, physiology, and life-history strategies. Despite the growing recognition of the importance of NCEs in biological control, most studies focus on cues from actively feeding predators, while the role of non-feeding stages, such as predator eggs, remains poorly understood. Here, we investigated whether eggs of the predatory mite *Phytoseiulus persimilis* function as intensity-dependent risk cues that influence the performance and population growth of the invasive spider mite *Tetranychus ludeni*.

RESULTS: Exposure to *P. persimilis* eggs significantly altered *T. ludeni* life-history traits in a density-dependent manner, even in the absence of direct predation. Increasing predator egg density reduced female longevity, reproductive rate, and total fecundity, delayed reproductive onset, but accelerated early egg production. Exposure to predator eggs also generated pronounced transgenerational effects that prolonged egg and female offspring development, reduced egg hatching, and lowered immature survival. These individual-level responses translated into strong population-level consequences, which significantly decreased the net reproductive rate (R_0), intrinsic rate of increase (r_m), and finite rate of increase (λ), but increased population doubling time (*Dt*) as predation stress intensified.

CONCLUSION: Our results demonstrate that predator eggs induce intensity-dependent NCEs that significantly suppress spider mite population growth. By extending fear-mediated effects from non-preying predator stages, this study broadens the functional scope of biological control and highlights the ecological significance of early predator cues in regulating pest populations.

Keywords: biological control; life-history strategy; *Phytoseiulus persimilis*; population growth; predation stress; *Tetranychus ludeni*

1 INTRODUCTION

Predators manage prey populations not only through direct consumption but also via non-consumptive effects (NCEs), where the perception of predation risk alters prey behavior, physiology, and life-history strategies.[1–4] Such risk-induced responses can substantially suppress prey development and reproduction, often reducing population performance to an extent comparable to or even exceeding that caused by direct predation.[2,5–8] In agricultural systems, NCEs are increasingly recognized as a critical but underutilized component of biological control,[9–13] because predator presence alone can usually reduce pest damage by limiting feeding, slowing development, and constraining reproductive output.[2,5,10,14–17]

Prey rely on diverse sensory cues, including chemical, tactile, and visual signals, to assess predation risk and adjust their behaviors and physiology accordingly.[18–22] Among these, chemical cues are particularly important in mediating NCEs across taxa, as they persist in the environment and convey information about predator identity, proximity, and recent feeding history.[22–27] Prey responses to predator-derived cues are typically graded rather than binary (i.e., presence *vs.* absence), scaling with cue concentration or intensity and allowing prey to estimate the magnitude and immediacy of threat.[17,21,23,28–30] Stronger chemical cues may consistently elicit more pronounced antipredator responses, demonstrating that behavioral adjustments scale with cue intensity[21] and animals are capable of integrating environmental information to evaluate threat levels.[31,32] However, such cue-dependent risk assessment may induce trade-offs between

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predator avoidance and investment in growth, reproduction, and survivorship, imposing substantial physiological and demographic costs.[12,14,17,33,34]

Spider mites in the genus *Tetranychus* (Acari: Tetranychidae) are among the most destructive arthropod pests in agricultural and horticultural systems worldwide, causing substantial crop losses due to their high fecundity, short generation time, rapid population growth, and frequent evolution of acaricide resistance.[35–38] Among various *Tetranychus spp*., the cosmopolitan invasive spider mite *Tetranychus ludeni* Zacher is an increasingly important agricultural pest, widely distributed in tropical and subtropical regions and capable of year-round reproduction due to the absence of diapause.[39,40] Its high fecundity, short generation time, and ability to disrupt host-plant physiology make it a persistent threat in agroecosystems.[41–43] Biological control using predatory mites, particularly phytoseiid species such as *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) and *Neoseiulus californicus* McGregor (Acari: Phytoseiidae), forms a cornerstone of integrated pest management against spider mites.[44,45] Although *Tetranychus spp.* may readily evolve resistance to acaricides,[36,46,47] *T. ludeni* remains highly susceptible to predation by *P. persimilis*, highlighting the importance of biological control for sustainable management.[39]

Tetranychus mites are capable of detecting and responding to predator cues through changes in behavior, reproduction, and habitat use.[12,16,17,24,30,48–52] While previous studies have mostly focused on the consumptive impacts of predatory mites on spider mite populations through investigating the prey preference and functional responses,[53–59] or have focused on cues associated with actively feeding stages,[16,52,60,61] overlooking the possibility that non-feeding stages may also convey ecologically relevant risk information. Predator eggs, in particular, may function as early indicators of imminent predation, as they signal forthcoming emergence of mobile juvenile predators, and may release chemical or contact cues detectable by prey.[62,63] So far, whether spider mites perceive predator eggs as reliable cues of future predation risk, and whether prey responses scale with egg density, remains poorly understood.

In the current study, we investigated whether eggs of the predatory mite *Phytoseiulus persimilis* act as intensity-dependent non-consumptive stressors that alter the life-history traits and population performance of *T. ludeni*. By exposing spider mites to increasing densities of predator eggs while excluding direct predation, we tested whether predator egg cues (i) function as reliable indicators of predation risk, (ii) induce graded changes in survival and reproductive scheduling of adult females, (iii) generate transgenerational effects on offspring development and survival, and (iv) ultimately suppress population growth. This study linked egg cue intensity to individual- and population-level responses, addressed a critical gap in spider mite ecology, and highlighted the potential for fear-mediated effects from non-feeding predator stages to enhance biological control in agricultural systems.

2 MATERIALS AND METHODS

2.1 Mite colonies and environmental conditions

The colony of *T. ludeni* was obtained from a home garden in Palmerston North, New Zealand, and reared and maintained on bean plants *Phaseolus vulgaris* L. (Fabales: Fabaceae) in the laboratory. The predatory mite *P. persimilis* was obtained from BioForce Limited, Auckland and reared on two-spotted spider mite *T. urticae* on bean plants. These two colonies were kept in two separate bioassay rooms at 25 ± 1°C, and 14:10 h (light: dark) photoperiod, with a 40 ± 10% RH for *T. ludeni* and a 65 ± 10% RH for *P. persimilis*.

2.2 Experiment, data collection, and data calculation

Four treatments were established to quantify the effect of predation intensity on reproductive performances of *T. ludeni*: (i) high predation intensity – a leaf arena of 2 cm^2 with five predator eggs, (ii) moderate predation intensity – a leaf arena with three predator eggs, (iii) low predation intensity – a leaf arena with one predator egg, and (iv) no predation risk (control) – a leaf arena without any predator egg. There were 15 replicates for each treatment. To obtain predator eggs for the experiment, 30 mated females of *P. persimilis* were randomly collected from the colony and individually introduced onto a leaf square (4 cm × 4 cm) infected with 20 *T. ludeni* eggs and placed upside down on a water-saturated cotton pad in a Petri dish (9 cm diameter × 1 cm height). After laying eggs for 24 h, the predator was transferred to another leaf square as mentioned above. To prepare mated *T. ludeni*, quiescent female deutonymphs were randomly collected from the colony and individually paired with virgin males for 24 h to ensure that all females were mated. Virgin males developed from eggs laid by virgin females. Mated females that were one day old were selected for the experiments.

For each replicate, predator eggs of the desired number were carefully transferred into a leaf arena using a fine hairbrush. A mated *T. ludeni* female was then introduced onto the leaf arena to oviposit. After 24 h, *T. ludeni* female was transferred to a new leaf arena with the same predator egg density. The predator eggs were also removed from the leaf arena daily, and replaced with fresh eggs (< 24 h) prepared as mentioned above to maintain a constant egg age and density throughout the experimental period. The number of eggs laid by the *T. ludeni* female was daily recorded under a stereomicroscope (Leica MZ12, Germany). These procedures were repeated daily until the female died. We recorded the parameters, including the female longevity, pre-oviposition period (from the initial of experiment to the first egg laid), oviposition period (from the first to last eggs laid), total fecundity, reproductive rate (total fecundity divided by longevity), developmental periods of eggs (from oviposition to egg hatching) and offspring (from oviposition to adult emergence), egg hatching rate (number of larvae divided by number of eggs), and immature survival rate (number of adults divided by number of larvae). Newly emerged adults were sexed and removed from the leaf arena daily.

2.3 Statistical analysis

We calculated the life table parameters using data on daily survival and daughter production of females.[64] The intrinsic rate of increase (r_m, daughters/female/day) was calculated by solving the Lotka-Euler equation, $\sum e^{-r_m x} l_x m_x = 1$, where x is the pivotal age, l_x is the proportion of females surviving to age x, and m_x is the number of daughters produced per female at age x. Other life table parameters included the net reproductive rate ($R_0 = \sum l_x m_x$, daughters/female/generation), finite rate of increase ($\lambda = e^{r_m}$), mean generation time [$T = \log_e(R_0)/r_m$, days], and doubling time [$Dt = \log_e(2)/r_m$, days]. The bootstrap method with 50 000 bootstrap samples[65,66] was used to calculate the pseudo-values of a given parameter for each female in each treatment.

All data were analyzed using SAS software (SAS 9.4, SAS Institute Inc., Cary, NC). Rejection level of H_0 was set at $P < 0.05$. Data on the female longevity, oviposition period, oviposition rate (eggs/day), and total fecundity after ln(x) transformation were normally distributed (Shapiro–Wilk test, UNIVARIATE Procedure) and thus analyzed using an analysis of variance (ANOVA, GLM procedure) with a Tukey's Studentized Range (HSD) Test for multiple comparisons between treatments. However, other data were not normally distributed, thus a generalized linear model with a gamma distribution and a log-link function (GLIMMIX Procedure) was applied to analyze data on the pre-oviposition period, offspring development, and life table parameters, and a logistic linear model (GENMOD Procedure) with a binomial distribution and logit-link function was used to compare egg hatching and immature survival rates between treatments. An adjusted Tukey–Kramer test was performed for multiple comparisons. An asymptotic exponential model[67] was applied to fit the daily cumulative number of eggs: Cumulative eggs = $a/\{1 + \exp[-b(Age\text{-}Age_0)]\}$, where a is the maximum value of egg cumulation, Age_0 is the inflection point at which the instantaneous growth rate is maximized, b is the constant growth rate of the cumulation curve. The difference in b or Age_0 was compared between treatments,[68] i.e., if the 95% confidence limits (95% CLs) overlap, then there is no significant difference.

3 RESULTS

3.1 Effects of predation stress on adult survival and female reproduction

Females exposed to low predation stress (one predator egg) survived similarly with the control; however, those exposed to higher predation stress (i.e., three and five predator eggs) significantly shortened their longevity by 31.0% and 41.1%, respectively, compared to the control and low predation stress ($F_{3,60} = 12.48$, $P < 0.0001$) (Fig. 1). Females had a significantly longer pre-oviposition period when they were exposed to three or five predator eggs compared to the control ($F_{3,60} = 5.64$, $P = 0.0018$) (Fig. 2(a)), but a significantly shorter oviposition period compared to the control and that exposed to lower predation stress (i.e., 1 predator egg) ($F_{3,60} = 11.50$, $P < 0.0001$) (Fig. 2(b)). Exposure to predation stress regardless of the intensity significantly reduced the reproductive rate of females ($F_{3,60} = 8.72$, $P < 0.0001$) (Fig. 2(c)), and increasing predation stress significantly decreased the total fecundity of *T. ludeni* females by 27.9%, 52.8%, and 68.7%, respectively, compared to the control ($F_{3,60} = 13.40$, $P < 0.0001$) (Fig. 2(d)). Compared to the control, the proportion of egg cumulation was significantly faster when females were exposed to three predator eggs (nonoverlapping 95% CLs) and the schedule of maximum instantaneous growth rate was significantly early when females were exposed to three or five predator eggs (nonoverlapping 95% CLs) (Fig. 3).

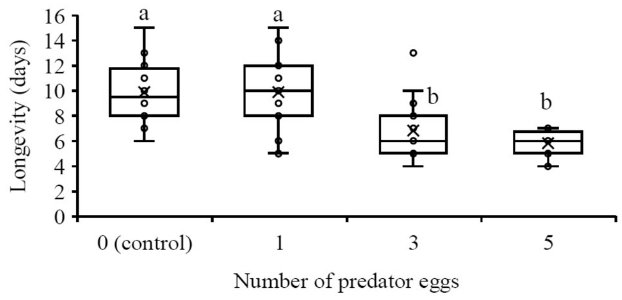

Figure 1. Longevity of *Tetranychus ludeni* females exposed to predation stress of different intensities. In each box plot, the line and '×' in the box show the median and mean, respectively; the lower and upper box lines indicate the interquartile range [25th (Q1) to 75th (Q3) percentiles]; the lower and upper whiskers represent the scores outside Q1 and Q3, respectively, and the open circles ('o') present the individual data points. Boxes with different letters are significantly different ($P < 0.05$).

3.2 Effects of predation stress on offspring fitness

Eggs laid by females exposed to five predator eggs significantly prolonged development compared to the control eggs ($F_{3,60} = 4.16$, $P = 0.0096$) (Fig. 4(a)), and female offspring required significantly longer time to complete development from egg to adulthood when their mothers were exposed to any intensity of predation stress than the control (Fig. 4(b)) ($F_{3,59} = 8.57$, $P < 0.0001$); however, predation stress had no significant impact on development of male offspring ($F_{3,59} = 2.00$, $P = 0.1243$) (Fig. 4(c)). Predation stress significantly decreased egg hatch rate

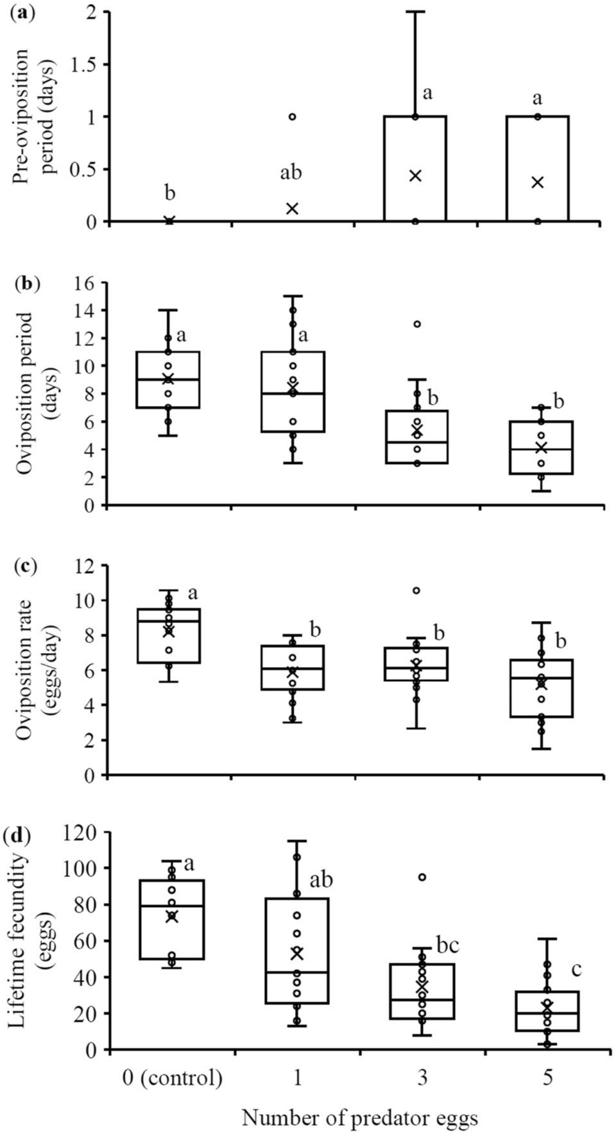

Figure 2. Pre-oviposition period (a), oviposition period (b), reproductive rate (c), and lifetime fecundity (d) of individual *Tetranychus ludeni* females exposed to predation stress of various intensities. In each box plot, the line and '×' in the box show the median and mean, respectively; the lower and upper box lines indicate the interquartile range [25th (Q1) to 75th (Q3) percentiles]; the lower and upper whiskers represent the scores outside Q1 and Q3, respectively, and the open circles ('o') present the individual data points. Boxes with different letters are significantly different ($P < 0.05$).

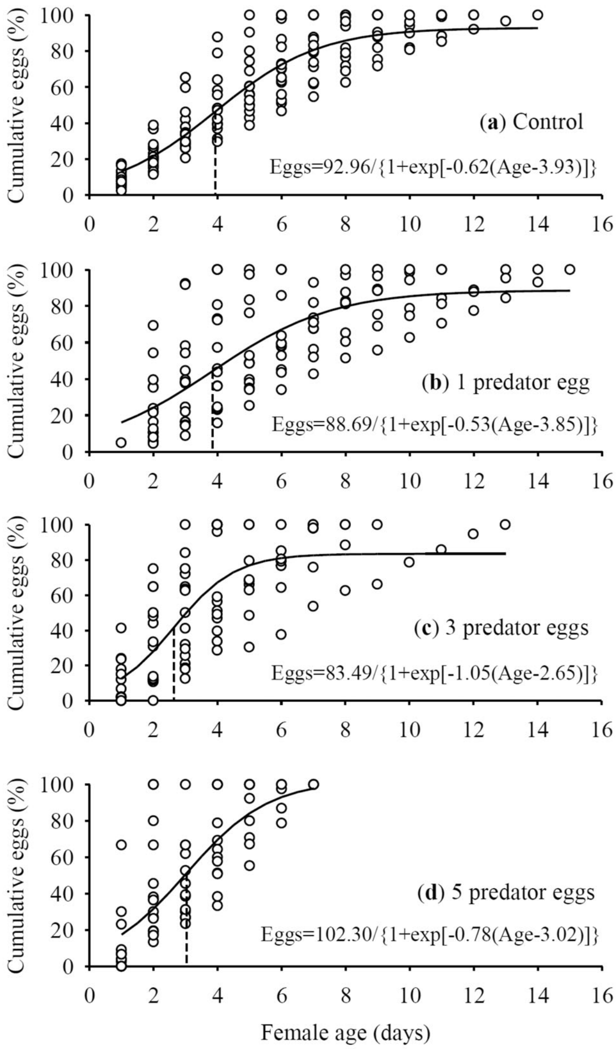

Figure 3. Proportion of egg cumulation over the reproductive period of *Tetranychus ludeni* females exposed to predation stress of various intensities: (a) Control, (b) one predator egg, (c) three predator eggs, and (d) five predator eggs. Solid line is the model prediction: Cumulative eggs = $a/\{1 + \exp[-b(Age\text{-}Age_0)]\}$, where a is the maximum value of egg cumulation, Age_0 is the inflection point at which the instantaneous growth rate is maximized (i.e., dash line), b is the constant growth rate of the cumulation curve. The open circles ('o') represent individual data points.

($x_3^2 = 84.42$, $P < 0.0001$) (Fig. 5(a)) and immature survival rate ($x_3^2 = 210.02$, $P < 0.0001$) (Fig. 5(b)).

3.3 Effects of predation stress on population growth

Exposure to predation stress and increasing its intensity significantly decreased the net reproductive rate (R_0), intrinsic rate of increase (r_m), and finite rate of increase (λ), but significantly increased the doubling time (Dt) of *T. ludeni* population (Table 1). The generation time (t) was significantly longer under predation stress of one predator egg compared to other treatments, and it was significantly longer under control conditions than under the higher predation stress of five predator eggs (Table 1).

4 DISCUSSION

Our study demonstrates that predator-derived cues, even from non-feeding life stages, induced significant and intensity-dependent stress responses in the spider mite *T. ludeni*. By quantifying the impacts of predator egg density on mite physiology and demography, we show that non-consumptive effects (NCEs) fundamentally reshaped prey life-history strategies, imposed transgenerational costs, and ultimately suppressed population growth. These findings highlight the importance of integrating risk perception, beyond direct predation, into our understanding of predator–prey dynamics and biological control efficacy.

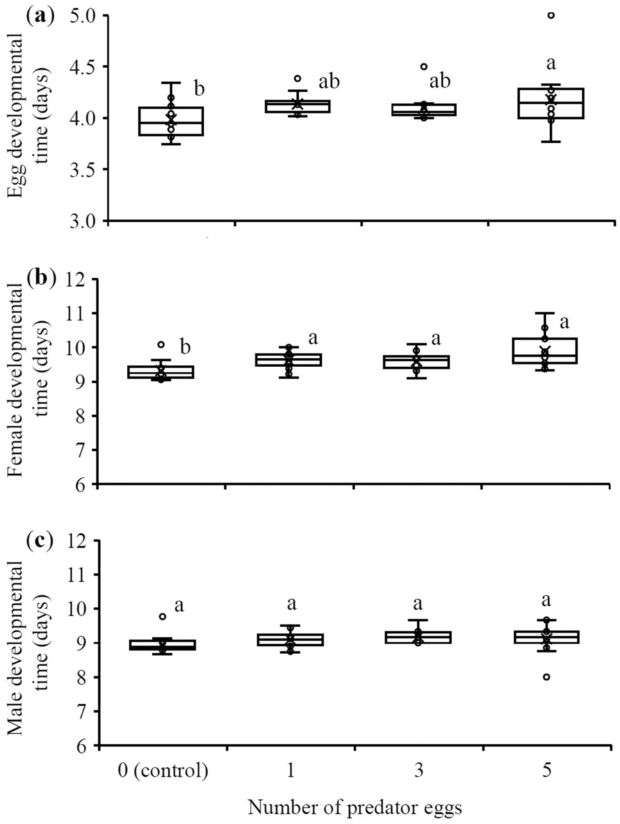

Figure 4. Developmental time of eggs (a), female offspring (b), and male offspring (c) of *Tetranychus ludeni* females exposed to predation stress of different intensities. In each box plot, the line and '×' in the box show the median and mean, respectively; the lower and upper box lines indicate the interquartile range [25th (Q1) to 75th (Q3) percentiles]; the lower and upper whiskers represent the scores outside Q1 and Q3, respectively; and the open circles ('o') present the individual data points. Boxes with different letters are significantly different ($P < 0.05$).

4.1 Predator eggs function as reliable, intensity-dependent cues of non-consumptive predation stress

Results of the present study show that the presence of eggs of predatory mite *P. persimilis* significantly shortened *T. ludeni* longevity (Fig. 1), suppressed reproduction (Fig. 2), delayed egg and female development (Fig. 4(a), (b)), and decreased egg hatching and immature survival (Fig. 5), and such negative impacts on prey performances usually increased with the number of predatory eggs. These results may have significant implications. First, predator eggs may serve as reliable indicators of imminent predation threat, thereby providing early warning signals that allow prey to adjust life-history strategies before direct encounter or consumption occurs.[62,63] It is well known that prey may detect predator-borne cues including chemicals that dissipate from predators and their products, such as eggs, excreta, and pheromones (e.g., 24, 48, 50). In fact, spider mites could perceive and

Table 1. Life table parameters of *Tetranychus ludeni* females exposed to predation stress (PS) of various intensities: net reproductive rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), generation time (T), and doubling time (Dt)

PS	R_0 (daughters)	r_m (daughters/female/day)	λ	T (days)	Dt (days)
Control	52.37 ± 0.26 a	0.3227 ± 0.0001 a	1.3808 ± 0.0013 a	13.27 ± 0.03 b	2.14 ± 0.01 d
1 egg	41.49 ± 0.53 b	0.2722 ± 0.0008 b	1.3128 ± 0.0010 b	13.69 ± 0.05 a	2.55 ± 0.01 c
3 eggs	20.94 ± 0.22 c	0.2499 ± 0.0006 c	1.2839 ± 0.0008 c	12.17 ± 0.03 bc	2.77 ± 0.01 b
5 eggs	14.75 ± 0.19 d	0.2219 ± 0.0011 d	1.2485 ± 0.0015 d	12.12 ± 0.04 c	3.12 ± 0.02 a
$F_{3,60}$	3072.38	2077.70	2393.00	443.25	2085.34
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

For each parameter, means (± SE) followed by different letters are significantly different (Adjusted-Tukey test: $P < 0.05$).

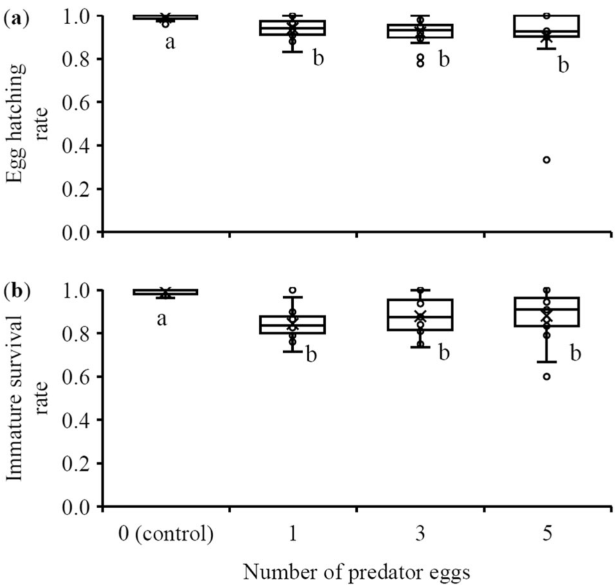

Figure 5. Egg hatching rate (a) and immature survival rate (b) when the ovipositing *Tetranychus ludeni* females were exposed to predation stress of different intensities. In each box plot, the line and '×' in the box show the median and mean, respectively; the lower and upper box lines indicate the interquartile range [25th (Q1) to 75th (Q3) percentiles]; the lower and upper whiskers represent the scores outside Q1 and Q3, respectively, and the open circles ('o') present the individual data points. Boxes with different letters are significantly different ($P < 0.05$).

assess future predation risk even in the absence of active predators.[16,52,60,61,69,70] Second, predator eggs alone elicited strong NCEs on *T. ludeni*. Our finding directly addresses a key gap identified in previous studies on spider mites, which have largely focused on predator feeding stages.[16,52,60,61] Third, the strong prey responses proportional to the density of predator eggs indicate that as reported in other *Tetranychus* species,[16,17,30,52,71] *T. ludeni* interpreted predator cues as a gradient of predation threat rather than a binary (presence *vs* absence) signal. Such early-stage risk perception allows prey to integrate predator cue intensity to estimate threat proximity, magnitude, and severity[17,21–23,30] before predators become mobile or consumptive.

4.2 Predation stress reshapes female life-history strategies through accelerated but costly reproductive scheduling

Exposure to predator egg cues under moderate to high predation stress (i.e., three and five predator eggs) substantially induced significant changes in the reproductive scheduling of *T. ludeni* females, characterized by the early acceleration of egg accumulation (Fig. 3), even though the late onset of reproduction (Fig. 2(a)). These adjustments in reproductive trajectories likely represent stress-induced reproductive compensation or terminal investment strategies, whereby individuals increase immediate reproductive effort when future survival or reproductive opportunities are uncertain.[29,72–75] In arthropods, predator-induced stress frequently triggers shifts toward earlier reproduction, reflecting an attempt to secure reproductive output before potential death.[17,76]

However, despite this apparent compensation, accelerated reproduction was accompanied by substantial costs. Compared to the control, *T. ludeni* females exposed to moderate to high predation stress significantly shortened their longevity by >30% (Fig. 1) and oviposition period by >40% (Fig. 2(b)), and reduced the daily reproductive rate by >17% (Fig. 2(c)) and total fecundity by >50% (Fig. 2(d)), suggesting that predation stress induced sustained stress in prey and compromised their fitness.[6] The earlier prey death and decreasing reproductive performances could be attributed to physiological and behavioral changes induced by NCEs, such as the energetic costs of risk avoidance,[77,78] decrease of foraging rate or food intake,[25,79,80] and increase of oxidative damage.[33] In addition, predator cues may affect prey through physiological pathways by inducing stress hormones,[3,74,81] which divert their resource allocation to other physiological processes that may translate into lower survivorship[14,17,34] and reproduction.[12,17,82] The shortened survival and reduced reproduction are expected to minimize the damage of *T. ludeni* to the infested crops.[12]

4.3 Predator-induced maternal stress induces transgenerational fitness costs

The legacy of maternal predation stress extended to the next generation, imposing fitness costs, thereby amplifying the population-level impact of NCEs. The delayed egg development (Fig. 4(a)), and prolonged development of female offspring (Fig. 4(b)) and reduced survival of eggs and immatures (Fig. 5) across all stress levels provided strong evidence for transgenerational phenotypic programming. Maternal stress alters offspring phenotype via several mechanisms, including changes in yolk hormone (e.g., ecdysteroid) or nutrient provisioning, deposition of maternal mRNAs, or epigenetic modifications.[83–85] This prolonged development was likely due to the maternal stress transmission, as even short-term gestational stress of the mother can override or interact with previous experiences to shape offspring performance.[74,84,86] These transgenerational effects ensure that the risk impact of predator cues persists well beyond the lifespan of the initially exposed individuals.

Interestingly, immature developmental delay in *T. ludeni* under predation stress is sex-specific, affecting female but not male offspring (Fig. 4(b), (c)). This pattern suggests a differential sensitivity or investment between sexes, with female offspring bearing greater costs of maternal stress. Sex-specific responses to predation stress have been reported previously in spider mites,[12,17,87] and other arthropods,[78,88,89] and may reflect differences in body size, energetic requirements, or exposure to risk during feeding and oviposition.[90,91] In spider mites, females are larger, more sedentary during feeding and oviposition, and nutritionally richer, making them more profitable and susceptible targets for predators.[92] In contrast, males are smaller and can engage in defensive behaviors to reduce predation risk.[93] Consequently, mothers under stress may therefore invest differently in daughters, who carry the direct burden of future egg production, or daughters may be more sensitive to the same maternal signals. The slowed development in daughters may be a conservative strategy, reducing their activity and visibility during vulnerable juvenile stages, but it also delays their entry into the reproductive pool, further inhibiting population growth.

4.4 Non-consumptive stress suppresses population growth

Although reproductive acceleration in predation-stress females of *T. ludeni* might provide a short-term buffering at the individual level (Fig. 3), its population-level consequences were strongly negative. As shown in Table 1, all life table parameters associated with population growth (R_0, r_m, and λ) significantly declined with increasing predation stress, while doubling time (Dt) significantly increased, indicating slower population expansion. These results demonstrate that NCEs alone were sufficient to substantially slow population expansion, even in the absence of direct predation. Such findings agree with those of previous studies that fear-mediated effects can rival or exceed consumptive effects in regulating prey populations.[2,7,8]

The discrepancy between individual-level reproductive acceleration and population-level decline in *T. ludeni* highlights the cumulative nature of physiological stress. The reduced longevity (Fig. 1), constrained fecundity (Fig. 2), and impaired offspring performance (Figs. 4 and 5) collectively limit the long-term growth potential of *T. ludeni* populations (Table 1). Similar patterns have been reported in other predator-spider mite systems, where predator cues suppressed population growth across multiple generations.[12,87] These results reinforce the conclusion that NCEs contribute to pest suppression not by directly eliminating individuals, but by altering life-history trajectories in ways that inhibit the population growth rate.

4.5 Predator eggs expand functional scopes of biological control through fear-mediated population suppression

We demonstrate that predator eggs of *P. persimilis*, as a precursor to juvenile predators, created a sustained background risk that could suppress pest populations before predators reach high densities. Similar fear-mediated suppression has been documented in other agricultural systems, where predator cues reduced herbivore feeding, reproduction, and population growth.[13,15] Thus, predators may exert dual control, i.e., direct predation by active stages and fear-mediated suppression via cues from eggs and other non-feeding stages. These NCEs effectively broaden the functional role of predators across their own life cycle, leading to more efficient and sustainable pest management.[7,9] For *Tetranychus* species, the notorious pests with rapid acaricide resistance development,[36,46,47,94] incorporating NCEs into biological control strategies may enhance pest population suppression while reducing reliance on chemical inputs. Recognizing predator eggs as functional contributors to pest control broadens the scope of predator efficacy and underscores the importance of predator establishment, persistence, and reproductive activity in agroecosystems. Future strategies could consider early or inoculative releases of predators to establish this 'landscape of fear' before pest populations escalate, optimizing the synergy between consumptive and non-consumptive effects for more resilient and effective biological control.

5 CONCLUSION

Predation stress induced by *P. persimilis* eggs generates strong, cue intensity-dependent NCEs on spider mite *T. ludeni* development, survival, and reproduction, thereby altering prey life histories. Our results show that *T. ludeni* females can perceive and assess future predation risk and proactively adjust life-history strategies. These responses involve shifts in resource allocation among growth, maintenance, and reproduction, which accelerate the initial reproduction but impose substantial fitness costs, including reduced survivorship and fecundity, highlighting the importance of physiological stress pathways in mediating nonlethal NCEs. Predation stress also elicited sex-specific responses, with female offspring exhibiting greater sensitivity to prolong development than males. This pattern likely reflects female-biased body size, higher energetic demands associated with egg production, and increased exposure to risk during sedentary feeding and oviposition. Therefore, incorporating early NCEs and predation stress intensity into assessing the potential of predators in suppressing prey populations fills a critical gap in spider mite ecology and highlights the ecological significance of fear-mediated effects in agricultural systems. Accounting for these NCEs will improve predictions of pest population dynamics and enhance biological control strategies. Nevertheless, although the predator egg densities used in this study were designed to create a controlled gradient of predation risk, their direct correspondence to field densities remains to be quantified. Future studies should link natural predator oviposition patterns with prey responses under greenhouse or field conditions to evaluate the applied significance of these non-consumptive effects.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

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