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Temperature Stress Induced Phenotypic Plasticity of *Spodoptera litura* (Lepidoptera: Noctuidae)

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ABSTRACT

Spodoptera litura (Fabricius), a highly damaging polyphagous pest, significantly affects crops in temperate and sub-tropical regions. This study investigates the impact of thermal stress exerted across different developmental stages on the phenotypic plasticity of *S. litura*, focusing on adult body size and weight. Field populations were reared in controlled conditions (27±1°C) and subjected to two higher temperature stress (42 ºC for 4 hours) and (46 ºC for 1 hour) for short and long-term duration. Results showed significant reductions in body size and weight of both male and female adults under increased temperature and duration of exposure. Exposure of early developmental stages *viz*., eggs and larvae resulted in severe reduction of size and weight in adults of female and male respectively. These findings indicate that early developmental stages are more susceptible to thermal stress, likely due to critical growth periods. The study highlights the vulnerability of *S. litura* to extreme temperature fluctuations and underscores the ecological implications of climate change on insect populations. Elevated temperatures lead to adaptive responses prioritizing survival over growth and development. Understanding these responses is crucial for developing sustainable pest management strategies and enhancing agricultural resilience amidst global climate challenge.

Keywords: Thermal stress, *Spodoptera litura*, body size, body weight, phenotypic plasticity, climate change.

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INTRODUCTION

Spodoptera litura (Fabricius), commonly known as the tobacco cutworm, is a highly damaging polyphagous pest affecting a wide range of crops, vegetables, and ornamental plants across temperate and sub-tropical regions in Asia, Australasia, and the Pacific Islands (Garad, Shivpuje, & Bilapate, 1984). It is known for causing significant defoliation damage ranging from 26% to 100% (Zhou, Chen, Deng, Chen, & Xu, 2007), highlighting its economic impact. Among the 112 host plants documented globally for *S. litura* (Moussa, Zaher, & Kotby, 1960), 60 are exclusive to India (Garad, Shivpuje, & Bilapate, 1984). This pest exhibits a remarkable capacity for invading new territories and adapting to diverse ecological conditions, facilitated by its nocturnal behavior, the high migratory capability of adult moths, and its ability to lay eggs on a broad spectrum of host plants (Chelliah et al., 1985). Infestations by *S. litura* result in substantial crop and economic losses due to its rapid reproduction and extensive host range (Sharma et al., 2014).

As poikilothermic organisms, insects' developmental rates are profoundly influenced by external temperature conditions, making temperature a critical environmental factor affecting their behavior, distribution, development, survival, and reproduction (Bale et al., 2002). The Intergovernmental Panel on Climate Change (2014) predicts a global temperature rise of 1.5-4.5 °C by the end of the century, with India expected to experience increases of 1.7 °C during the kharif season and 3.2 °C during the rabi season by 2070, impacting agricultural productivity and insect population dynamics (Gupta, 2011). Ectothermic animals, including insects like *S. litura*, exhibit life-history traits that are strongly influenced by thermal conditions (Precht, Christophersen, Hensel, Larcher, & Jankowsky, 1973). With rising temperatures, organisms often respond ecologically by altering their body size, timing of life cycle events, and geographic distribution (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). This thermal influence on body size in ectotherms is primarily mediated through effects on development rates and metabolism (Atkinson, 1994), traits critical to insect fitness, physiology, behavior, and ecology (Henry, Ma, & Roitberg, 2009). Research indicates that higher temperatures generally lead to smaller insect body sizes, which can correlate with reduced fecundity (Kant, Minor, Trewick, & Sandanayaka, 2012).

In general, larger body size confers advantages such as increased reproductive success, better mate access, and improved resource acquisition (Blanckenhorn, 2000). Therefore, a decrease in adult body size may indicate a reduction in overall fitness to some extent (Hoffmann & Loeschcke, 2006). Despite these insights, the specific impacts of short and long-term temperature stress on the developmental stages of *S. litura* remain unexplored. Understanding how *S. litura* populations respond to thermal stress is crucial for predicting the effects of climate change on their distribution, phenology, and population dynamics, especially in regions experiencing extreme heat events. This study aims to investigate the effects of short and long-term thermal stress on phenotypic plasticity focusing on body size and weight of adult male and female *S. litura*, contributing to a deeper understanding of their adaptive responses to environmental challenges.

MATERIALS AND METHODS

Rearing of *Spodoptera litura*

The field population of *S. litura* was collected and mass multiplied in the insect culture room of the Insect Physiology and Molecular Biology Laboratory, Entomology Division, ICAR-IARI, New Delhi. The collected larvae were reared on a meridic diet and adults on the honey solution (Sagar, Thillainayagam, Keerthi, Sujatha, & Chander, 2022), and the whole culture was maintained at an optimum temperature of 27±1 °C with 65±5% relative humidity, and 14:10 h light: dark cycle.

Exposure of *Spodoptera litura* to temperature stress

To examine the effect of thermal stress on the body size and weight of adult males and females of *S. litura*, all the developmental stages were subjected to two higher temperature regimes: 42 ºC for 4 hours and 46 ºC for 1 hour, under both short and long-term exposure conditions, with a relative humidity (RH) of 65±5%. The control population was maintained at 27±1 °C, 65±5% RH. These temperature regimes and exposure durations were chosen based on the weather conditions during the Kharif season in Delhi (June-July), where temperatures typically reach a maximum of 42 ºC for 3-4 hours. In anticipation of future climate scenarios, a higher temperature of 46 ºC was also included to assess potential impacts of extreme heat events.

The selected developmental stages for both short and long-term exposure included freshly laid eggs (100 eggs, ≤18 hours old), 4th instar larvae (100 larvae, ≤12 hours old), freshly formed pupae (100 pupae, ≤12 hours old), and newly emerged adults (30 males and females, ≤12 hours old). Short-term exposure involved a one-time exposure of the selected stages as mentioned above, while long-term exposure consisted of multiple exposures over 2, 4, 2, and 2 days for eggs, larvae, pupae, and adults, respectively, at both temperature regimes. After thermal stress, the exposed insects were maintained under optimal conditions (27±1 °C, 65±5% RH) with meridic diet for larvae and honey solution for adults.

Assessment of survival rates across developmental stages of *Spodoptera litura* after exposing to different hot events

Survivability of different developmental stages of *S. litura* was calculated after short and long-term exposure to thermal stress. Survival rate of eggs, larvae, pupae and adults was calculated by percentage hatching success from stressed eggs, percentage pupae formed from stressed larvae and percentage adult emergence from stressed pupae, respectively. For adults, immediate survival was calculated by determining the percent survival following a recovery period of 1 hour post-thermal stress at 27±1 ºC. The survival rate of stressed eggs, larvae, and pupae was calculated using the formula:

$$\text{Survival rate } (\%) = \frac{\text{No.of emerged individuals in the next stage after treatment})}{\text{No.of individuals in treatment stage}} \times 100$$

For adult survival rate, the formula used was:

$$\text{Adult Survival Rate } (\%) = \frac{\text{No. of survived adults}}{\text{Total no. of adults exposed}} \times 100$$

Adult body size and weight of male and female insects of *Spodoptera litura* after exposing developmental stages (egg, larvae, pupa) and adults to different hot events

The freshly emerged male (N=10 each for size and weight) and female adults (N=10 each for size and weight) from stressed eggs, larvae, pupae, and stressed adults (≤24 hours old) were directly used for measurement of body size and weight. For both single and multiple stress treatments, only newly emerged adults (≤12 hours old) were selected to ensure consistency in age during measurements. For measuring the size, male and female adults were killed, stretched and pinned on the surface of the thermocol and by using ruler (0-15cm) the wingspan of the adult insects were measured and recorded in centimetre (cm).For recording weight, to avoid the movement of the insects in weighing balance, adults were anaesthetized using refrigerator for 10-15 minutes. Using digital weighing-balance (Citizen CX-120, sensitivity of 0.1 mg) the weight of the adult insects from different treatments and control were recorded and expressed as grams (g).

Statistical analysis

The data on survivability of different stages, body size and weight of male and female adults of *S. litura* was analysed statistically using a two-way ANOVA in a completely randomized design to examine the effects of temperature treatments, stage, and their interactions. Significant differences were identified using Tukey's HSD ($p < 0.05$) and represented as mean ± SE using SPSS v 16.0.

RESULTS

Survival rates of *Spodoptera litura* after exposure to short and long-term thermal stress

The survival rate of *Spodoptera litura* was significantly affected by temperature treatments ($F_{4,1625} = 29.36$; $P < 0.0001$), developmental stages of exposure ($F_{4,1625} = 66.39$; $P < 0.0001$), and the interaction between temperature and developmental stages ($F_{16,1625} = 3.42$; $P < 0.0001$). Among the different temperature treatments, the 46°C 1-hour multiple stress treatment resulted in the lowest survival rate across all life stages, including eggs, larvae, pupae, and male and female adults ($F_{4,325} = 20.541$; $P < 0.0001$), compared to the control group ($F_{4,325} = 3.582$; $P = 0.007$). The larval stage exhibited the lowest survival rate ($F_{4,495} = 44.853$; $P < 0.0001$) at only 16.2%, while the pupal ($F_{4,495} = 10.335$; $P < 0.0001$) and adult female stages ($F_{4,70} = 2.696$; $P = 0.038$) demonstrated higher tolerance to thermal stress, with survival rates of 64.8% and 54%, respectively, under the same treatment. The egg ($F_{4,495} = 10.156$; $P < 0.0001$) and male adult stages ($F_{4,70} = 2.962$; $P = 0.025$) showed intermediate survival rates of 55.8% and 48%, respectively, at 46°C 1-hour multiple stress treatment. Similar trends in survival rates across developmental stages were observed under other temperature treatments (Table 1).

Table 1. Effects of short and long-term temperature stress on different developmental stages on the survival rate of *Spodoptera litura.*

Treatments	Egg	Larva	Pupa	Adult (Male)	Adult (Female)
Control	86.4±1.77aA	81±2.71aA	90±0aA	90±0aA	90±0aA
42˚C- 4 hours Single stress	73.8±3.47abAB	50.4±4.48bB	82.8±2.45abA	72±9.62abAB	84±6abA
42˚C- 4 hours Multiple stress	70.2±3.74bAB	46.8±4.51bB	77.4±3.13bA	72±9.62abAB	72±9.62abAB
46˚C- 1 hour Single stress	63±4.14bcA	21.6±3.84cB	72±3.61bcA	54±11.78abA	66±10.64abA
46˚C- 1 hour Multiple stress	55.8±4.39cA	16.2±3.47cB	64.8±4.06cA	48±12bA	54±11.784bA

Mean± Standard Error (SE) values of survival rate (%) of *Spodoptera litura*, after exposure of egg, larva, pupa, male and female adults to short and long-term temperature stress (27˚C (Control), 42 – 4 hours (single stress), 42 – 4 hours (Multiple stress- 2,4,2 and 2 days for egg, larva, pupa male and female adults respectively), 46 – 1 hour (Single stress) and 46˚C- 1 hour (Multiple stress- 2,4,2 and 2 days for egg, larva, pupa male and female adults respectively). Different lowercase letters indicate significant differences among temperature treatments in a particular stage, uppercase letters indicate significant differences among different stages for a particular temperature treatment (Tukey's HSD test, P<0.05).

Adult body size of *Spodoptera litura* after exposure to short and long-term thermal stress

The adult female size of *S. litura* was significantly influenced by both developmental stages of exposure (F3,80 = 32.655, P < 0.0001) and thermal stress treatment (F4,80 = 49.665, P < 0.0001), as well as their interaction (F12,80 = 3.251, P = 0.001) (Table 2). Female size decreased gradually with increasing temperature across all developmental stages. Females emerging from thermally stressed eggs ($F_{4,20}$ = 17.388, P < 0.0001) showed significantly smaller sizes with rising temperature, while the reduction in size was less pronounced when exposed at the adult stage ($F_{4,20}$ = 3.588, P = 0.023). Females emerging from pupal and larval stress stages exhibited relatively larger sizes compared to those from stressed eggs. The smallest females were observed under the 46˚C-1-hour multiple stress treatment (F3,16 = 16.872, P < 0.0001) compared to other temperature treatments across all stressed stages (Fig. 1).

Table 2. Analysis of variance (ANOVA) for the effects of developmental stage and temperature on size and weight of male and female *Spodoptera litura.*

Parameters	Source[a]	df	Mean square	F	P
Size of female (cm)	Stage	3, 80	0.292	32.655	<0.0001
	Temperature	4, 80	0.444	49.665	<0.0001
	Stage × Temperature	12, 80	0.029	3.251	0.001
Size of male (cm)	Stage	3, 80	0.304	73.189	<0.0001
	Temperature	4, 80	0.139	33.578	<0.0001
	Stage × Temperature	12, 80	0.037	8.952	<0.0001
Weight of female (g)	Stage	3, 80	0.036	51.167	<0.0001
	Temperature	4, 80	0.024	34.23	<0.0001
	Stage × Temperature	12, 80	0.002	2.832	0.003
Weight of male (g)	Stage	3, 80	0.001	3.626	0.016
	Temperature	4, 80	0.002	13.868	<0.0001
	Stage × Temperature	12, 80	0.0000889	0.533	0.887

[a]Temperature levels are 27 (Control), 42 – 4 hours (Single stress), 42 – 4 hours (Multiple stress), 46 – 1 hour (Single stress) and 46˚C- 1 hour (Multiple stress); the stages are Egg, Larva, Pupa, female adult and male adult for body size and weight of *Spodoptera litura.*

Male adult size was significantly influenced by the developmental stage of exposure (F3,80= 73.189; P<0.0001), temperature treatment (F4,80= 33.578; P<0.0001), and their interaction (F12,80= 8.952; P<0.0001) (Table 2). Among developmental stages, adults (F4,20= 0.500; P=0.736) and pupae (F4,20= 2.20; P=0.106) showed non-significant differences in response to different temperature treatments, while larvae (F4,20= 38.037; P=0.0001) were most affected, exhibiting greater size reduction with higher thermal stress exposure and duration. Male adults emerged from stressed eggs and pupae were larger than those from stressed larvae. The smallest adult male size occurred in the 46°C-1-hour multiple stress treatment (F3,16=34.55; P=0.0001) across all developmental stages, compared to other treatments (Fig. 2).

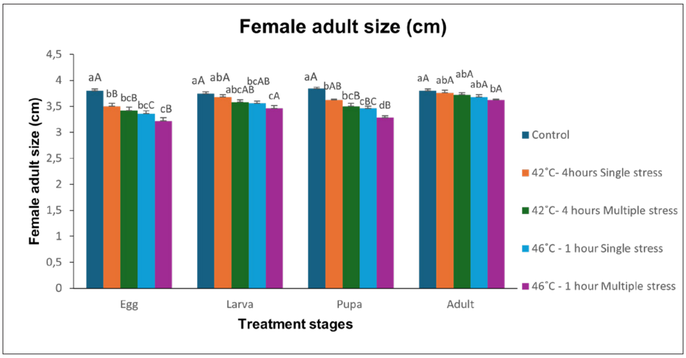

Figure 1. Effects of short and long-term temperature stress in various stages on female adult size (cm) of *Spodoptera litura.*

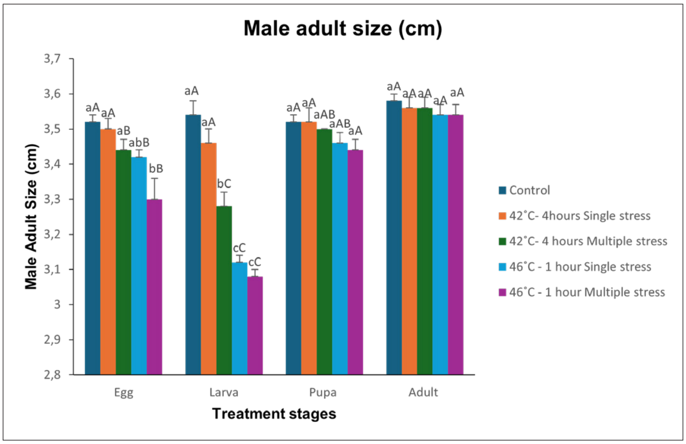

Figure 2. Exposure of different stages of *Spodoptera litura* to short and long-term temperature stress on male adult size (cm).

Adult body weight of *S. litura* after exposure to short and long-term thermal stress

The weight of female adults was significantly influenced by the stages of exposure (F3,80= 51.167; P<0.0001), thermal stress treatments (F4,80= 34.23; P<0.0001), and their interaction (F12,80= 2.832; P=0.003) (Table 2). Increasing temperature and duration led to a significant reduction in weight at all developmental stages. Females from stressed eggs (F4,20= 6.553; P<0.002) and larvae (F4,20= 33.871; P<0.0001) had notably lower weights than those from adults (F4,20= 2.826; P=0.052) and pupae (F4,20= 10.478; P=0.0001). The 46°C-1-hour multiple stress treatment ($F_{3,16}$

= 31.439, P < 0.0001) caused a significant decrease in weight across all exposure stages, except for adults, where no significant difference was observed among the different temperature treatments (Fig. 3).

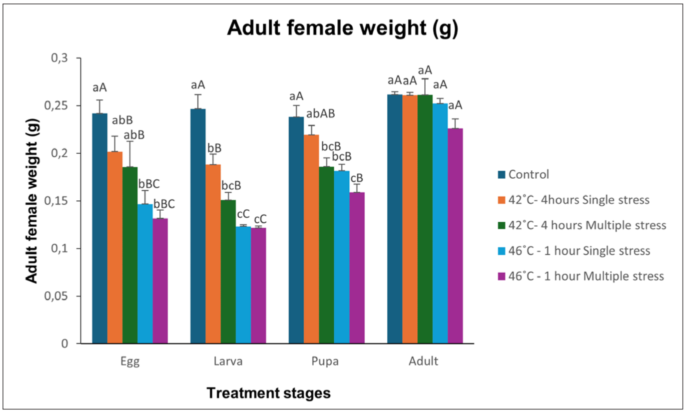

Figure 3. Changes in adult female weight in relation with short and long-term thermal stress on various stages of *Spodoptera litura*.

The weight of male *S. litura* adults was significantly affected by both the developmental stage of exposure (F3,80= 3.626; P=0.016) and thermal stress treatment (F4,80= 13.868; P<0.0001), while their interaction (F12,80= 0.533; P=0.887) had no significant impact (Table 2). As temperature and duration increased, male adult weight gradually decreased. In the pupal stage (F4,20= 2.88; P=0.049), there were no significant weight differences under different temperature treatments, whereas significant differences were observed in other stages. Larval exposure (F4,20= 5.472; P=0.004) to thermal stress had the most substantial effect on male adult weight. The 46°C-1-hour multiple stress treatment (F3,16= 1.977; P=0.158) resulted in the lowest male adult weight across all stages compared to other thermal stress treatments (Fig. 4).

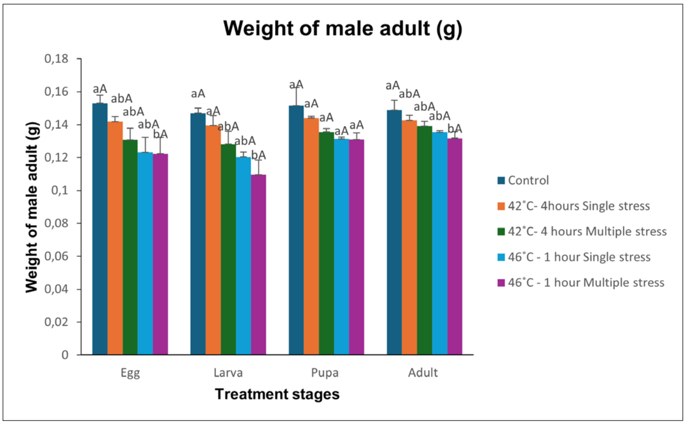

Figure 4. Effect of temperature stress both short and long-term exposure in different developmental stages on male adult weight of *Spodoptera litura*.

CONCLUSIONS AND DISCUSSION

Our study aimed to investigate the impact of thermal stress on phenotypic plasticity focusing on body size and weight of *S. litura* adults across different developmental stages. The results confirm the general principle that "hotter conditions yield smaller insects," a concept supported by previous research (Atkinson, 1994, Kingsolver & Huey, 2008). Under thermal stress, insects prioritize survival and reproduction over growth once they reach an optimal size (Joern & Behmer, 1997). This study reveals that increasing temperature and exposure duration significantly reduce the size of both male and female *S. litura* adults.

The maximum reduction in size was observed in female adults that emerged from eggs and pupae subjected to thermal stress, whereas the greatest reduction in size for males was observed in those that emerged from thermally stressed larvae. Under thermal stress, the egg stage is more critical for females due to its influence on early development, while the larval stage is vital for males, as it is a key growth phase affecting feeding and development. The most severe reduction in size for both sexes occurred under the 46°C multiple stress treatment for 1 hour over 4 days across all developmental stages. These results are consistent with similar findings in other insects, such as *Nezara viridula* (Danks,1987), *Ophraella communa* (Chen, Zhou, Gong, He, & Huang, 2006), as well as in aphids and parasitoids (Smith, Mackay, & Lamb, 1998). Interestingly, female *S. litura* emerging from thermal stressed eggs and male *S. litura* emerged from stressed larvae were smaller compared to those from stressed pupae and adults. This suggests that early developmental stages are more susceptible to thermal stress, potentially due to the critical periods of growth and differentiation occurring during these stages. Elevated temperatures likely cause earlier maturity by affecting the cell differentiation rate more than the growth rate, resulting in smaller adult sizes (Radmacher & Strohm, 2010). Additionally, increased behavioral and physiological activities during thermal stress conditions contribute to reduced size and weight (Chown & Terblanche, 2006). Insects expend higher amounts of energy under thermal stress, resulting in these reductions (Gillooly, Brown, West, Savage, & Charnov, 2001). This is probably due to a trade-off between energy use and structural allocation, with more energy being directed towards metabolism and maintenance at higher temperatures (Van der Have & de Jong, 1996). Wonglersak, Fenberg, Langdon, Brooks, & Price (2020) also reported a decline in the wing length of Zygoptera, indicating that later-season emergents are smaller.

Our study further reveals that increased temperature and exposure duration significantly reduced the body weight of both female and male *S. litura* adults across all developmental stages, with the most pronounced weight reduction occurring during the larval stage. Specifically, the 46°C multiple stress treatment for 1 hour over 4 days resulted in the lowest recorded weights for both sexes, consistent with findings in other insects like *Aphis pisum* and *Aphis fabae* under thermal stress (Dixon, Chambers, & Dharma, 1982), *Toxoptera aurantii* (Murdie, 1969), and females of *Sogatella furcifera* and *Nilaparvata lugens* from stressed nymphs (Ma, Hu, & Cheng,1998). This significant weight reduction during the larval stage can be attributed to the high-energy demands of rapid growth and differentiation processes, which are compromised as energy is redirected towards basic metabolic functions and stress-coping mechanisms under elevated temperatures (Gillooly, Brown, West, Savage, & Charnov, 2001). The severe impact of the 46°C multiple stress treatment underscores the vulnerability of *S. litura* to extreme temperature fluctuations, a concern that is increasingly relevant in the context of climate change. As global temperatures rise, the frequency and intensity of thermal stressors are likely to increase, posing significant challenges for insect populations.

Our findings suggest that elevated temperatures impose significant stress on *S. litura*, causing marked reductions in both body size and weight across developmental stages. Such reductions are indicative of an adaptive response where energy allocation shifts towards survival and maintenance, rather than growth. This adaptation ensures immediate survival but may compromise long-term fitness, as smaller body sizes and reduced weights are often correlated with lower fecundity and reproductive success (Zhao, Chen, Guo, & Zhou, 2022). The correlation between smaller size and reduced fitness has been documented across various insect species, emphasizing the broader ecological and evolutionary impacts of climate-induced thermal stress (Chen, Zhang, & Chen, 1998). Future research should explore the heritability of these stress responses and potential adaptive mechanisms across multiple generations to better understand the resilience of *S. litura* and other insects to ongoing climate change.

Our study elucidates the profound impact of thermal stress on phenotypic plasticity of adult body size and weight across different developmental stages of the tobacco caterpillar, *S. litura*. We observed significant reductions in both male and female sizes and weights under increased temperature and duration of exposure, with egg and larvae displaying the highest sensitivity to thermal stress. The 46°C multiple stress treatment over four days induced the most severe reductions, highlighting the vulnerability of *S. litura* to extreme temperature fluctuations. In a nutshell, if the egg stage has experienced the thermal stress, the effect was reflected in the female adults while the larvae stage was exposed to thermal stress the pronounced effect was on male adults.

These findings underscore the ecological implications of climate change on insect populations, emphasizing adaptive responses prioritizing survival over growth and reproduction. However, such adaptations may compromise long-term fitness, as smaller body sizes often correlate with reduced fecundity. Our study contributes crucial insights into insect responses to environmental stressors, emphasizing the need for further research on adaptive mechanisms and evolutionary dynamics under changing climatic conditions. This knowledge is essential for developing sustainable pest management strategies and enhancing agricultural resilience in the face of global climate challenges.

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