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Heat Stress and Thermoregulation in Insects: Unveiling Molecular and Physiological Responses in Light of Climate Change

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Insects being poikilotherms rely on external temperatures to regulate their body heat that making them vulnerable to climate change as temperature fluctuations directly impact their growth, reproduction and survival as well as control their metabolic and physiological processes. Many

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insect species are in danger as global temperatures are increasing since they cannot physiologically adapt themselves for long exposure to high temperatures. This vulnerability is especially pronounced in species that have not evolved mechanisms to endure extreme heat, leading to potential population decline and disruptions in ecosystems Understanding the mechanisms of how insects manage heat stress is crucial for predicting their behaviour and biology in the scenario of a changing climate. This review delves into the genetic basis of thermoregulation in insects, exploring how genes influence their ability to cope with heat stress and regulate their internal body temperature in hot conditions through mechanisms such as heat shock proteins, metabolic adjustments, and behavioural changes. It also highlights gaps in current research and suggests future studies, emphasizing the need for comprehensive investigations into the molecular, genetic, and ecological aspects of thermoregulation. Advanced insights into insect thermoregulation will enhance our understanding of insect population dynamics and facilitate the development of effective pest management strategies, contributing to climate-resilient agriculture amidst the challenges posed by a changing climate.

Keywords: Thermoregulation; heat stress; heat shock proteins; reproduction; hormones; antioxidant enzymes; cuticular proteins.

1. INTRODUCTION

As insects are typically classified as ectotherms and poikilotherms, they possess physiological and behavioural mechanisms that allow them to thermoregulate to some extent, enhancing their performance in warm conditions [1]. The relationship between temperature and development rate has always strongly affected Insect population, distribution and diversity [2]. Temperature is among the most significant environmental variables that influence the physiological condition, behaviour and evolution of an insect. Being exposed to either extremely high or low temperatures can retard insect development through abiotic stress which may lead to abnormalities in insects [3]. The main factor responsible for the survival of individual organisms in warmer environments is tolerance towards high temperatures commonly referred to as heat tolerance [4]. Heat tolerance in insects arises from a complex interplay of internal physiological and biochemical mechanisms [5]. These include sensory and regulatory neuronal processes, cellular stress responses, and metabolic and hormonal adjustments. Additionally, heat tolerance relies on thermoregulatory physiological mechanisms, enabling insects to achieve a degree of endothermy [6]. Consequently, insects exposed to extreme temperatures (both high and low) employ various strategies to manage stress, such as avoiding extreme temperatures, regulating stress protein and oxidase activity and altering other physiological traits [7].

On the other hand, in overwintering insects, exposure to low temperatures leads to a decreased respiratory rate, diminished aerobic respiration, and damage to cell membranes, which in turn causes membrane lipid peroxidation [8]. Energy production, along with the synthesis of sugars, alcohols, and amino acids from fat metabolism and the tricarboxylic acid cycle (TCA cycle), enables these insects to withstand cold environments [9]. Moreover, insects develop cold resistance through mechanisms like freeze tolerance, freeze avoidance and the accumulation of polyols [10]. Conversely, exposure to high temperatures triggers physiological changes in insects that alter the cellular microenvironment, affecting cell structure, enzyme activity, and the spatial conformation of biological macromolecules. Thus, these modifications may have an effect on typical growth, development and survival [6].

In support of different biochemical factors, there are numerous genes, such as those encoding heat shock proteins (HSPs), heat shock transcription factors, the hsr-omega protein, and phosphoglucose isomerase, are upregulated in insects in response to heat stress [11]. The heat shock response, involving heat shock proteins, protects cells from damage in elevated temperatures [12]. Additionally, hormones play a role in modulating responses to high temperatures, influencing the physiology, development, and behaviour of insects [13]. It is known that insects are ectothermic species and have specific physiological processes that are significantly affected by ambient temperature. Despite evolutionary adaptability to various environmental conditions, extreme heat showed a substantial challenge to their survival, growth and development. When global temperature is

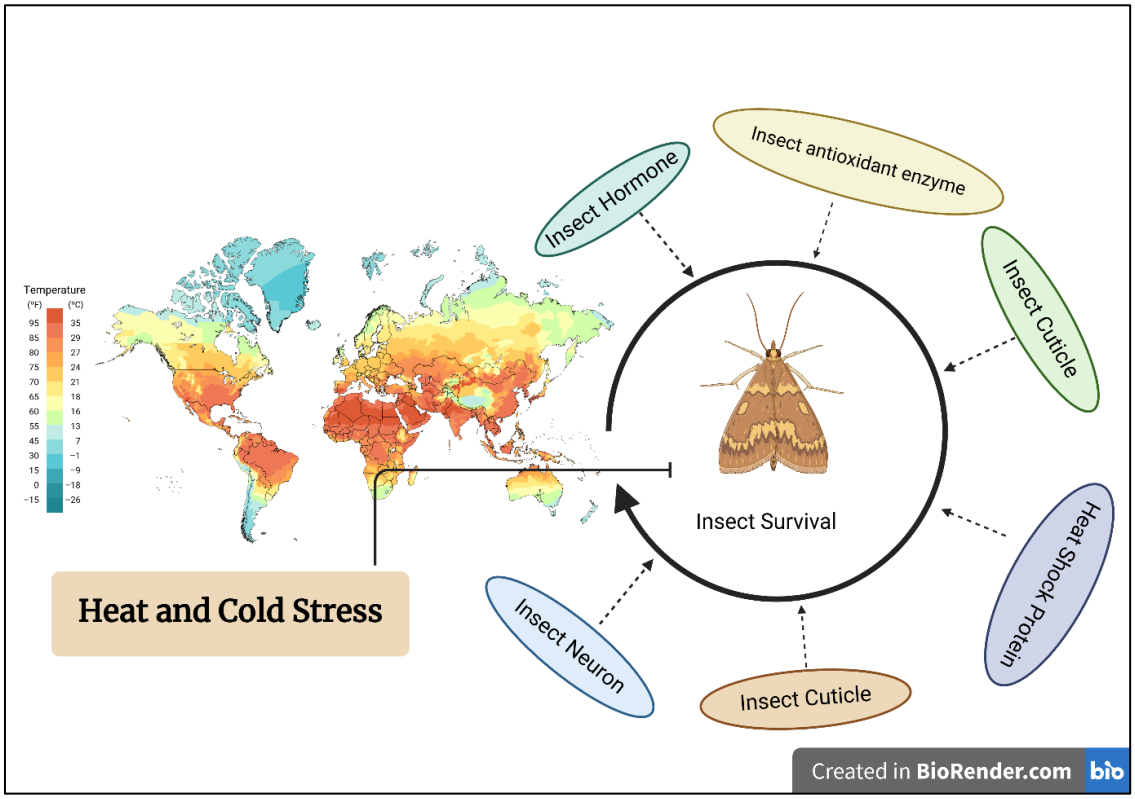

Fig. 1. The depiction of heat and cold stress tolerance in insects (Designed using Biorender online software- https://app.biorender.com) [14]

continuously rising, it is very important to understand how insects manage heat stress at the physiological level to better predict their responses to climate change to devise effective pest control and conservation strategies. This review explores the physiological mechanisms inside the insects that govern heat responses and confer heat tolerance in insects including metabolic adjustments to heat and thermoregulation processes.

2. IMPACT OF HEAT STRESS ON DEVELOPMENTAL BIOLOGY

Extreme temperatures are occurring more frequently due to climate change. One of the primary research projects now focuses on identifying which organisms can maintain their fitness and adapt to changing climates. In holometabolous insects, the impact of high temperatures on survival is known to vary depending on the life stage during which thermal stress occurs [15]. Research on heat-induced male sterility typically examines prolonged stress across various ages or acute stress in specific age groups [16]. Recent studies on the flour beetle, *Tribolium castaneum* reveal that fertility loss due to thermal stress depends on the life stage affected, with the pupal and immature adult stages being the most vulnerable. This suggests a critical period where heat stress significantly impacts fertility, warranting further research into thermal sensitivity across life stages [17].

Heat stress has been shown to extend the developmental stages of various insects, with long-lasting effects on subsequent generations. This phenomenon has been observed in species such as *Frankliniella occidentalis* [18], *Drosophila serrata* [19], *T. castaneum* [20], and *Dysaphis plantaginea* [21]. However, the degree of impact differs among insect species across generations. Extended developmental periods can lead to growth retardation under extreme temperatures [22]. However, insects have demonstrated resilience to thermal stress, as shown by their ability to recover over multiple generations, albeit with some developmental trade-offs [18]. It was observed that *Spodoptera frugiperda* gradually recovered from thermal stress across generations, with a significant reduction in developmental duration from the F_0 to F_2 generations [23].

3. IMPACT OF HEAT STRESS ON INSECT REPRODUCTION

Early investigations into the effects of rising temperatures on biodiversity mainly examined how thermal stress impacts the survival of insects [24]. While survival remains a crucial concern, it has been understood for approximately a century that high temperatures can also impair fertility in some species [25]. It was seen that fertility was the ability to produce offspring, in contrast to sterility. This concept also proves that the fertility factor is critical because complete sterility could have significant importance in a warming world [26-27]. The importance of fertility for population sustainability and thermal limits on insect fertility likely play a significant role in the observed declines in insect populations. Heat-induced sterility has been observed across various taxa, including crops [28] and livestock [7], suggesting that species that lose fertility at temperatures well below their lethal limits may pose major economic and conservation challenges, with potentially serious consequences for insect resilience to climate change.

In connection to the decrease in fertility of insects it was seen that in *Drosophila subobscura*, heat stress negatively impacts sperm motility and reduces fertility [29]. The thermal fertility limit denotes the temperature at which a species loses its ability to reproduce [28]. It has been also found that the developmental heat stress in the pomace fly, *Drosophila suzukii* decreases fertility, with females showing reduced ovary size and males having fewer sperm. However, heat-stressed females exhibit enhanced egg-to-adult viability under heat stress. Males are more severely affected, experiencing reduced sperm viability and increased chromatin degradation [30]. Also. In some insects, heat waves during the pupal stage significantly decrease male sperm production, resulting in a male-biased sex ratio in the subsequent generation [31]. In *Drosophila melanogaster* measurements in the testes and for proxies of sperm availability indicating the onset of adult reproductive capacity matched the expected heat-induced delay in completing spermatogenesis [16].

The impact of heat stress has been not only seen in insect pests it is also observed in pollinators too that the decline in sperm quality among bumble bee males is particularly concerning since most bumble bee queens are monandrous [32-33]. After hibernation, queens use the stored sperm in their spermatheca to fertilize eggs, producing diploid workers, while unfertilized eggs become males [30]. It has been seen that if a queen mates with a male exposed to heat stress, she may receive a poor-quality sperm supply. It means because of heat stress not only fertility is getting affected but it mainly affecting the sex ratio and reproductive efficiency [34]. In addition, the limits to insect fertility based on temperature alone are likely to underestimate the true effects of climate change on insect persistence, and the explicit incorporation of water regulation into our modelling will yield more accurate predictions of the effects of climate change on insect declines [35]. Male fertility is a crucial yet often neglected factor in examining the ecological and evolutionary effects of climate change have been proven on *Cotesia* sp, and parasitoid wasps (Pteromalidae) [28,31].

Heat stress not only impacts insect fertility but also disrupts mating behaviour. As climate warming continues, changes in mating behaviour could become crucial for population conservation through sexual selection. For example, a study on red flour beetles found that heatwaves reduced the ability of males to produce offspring by affecting their mating behaviour, leading to lower sperm count and viability [36-37]. It is well established that heat stress negatively influences both premating and post-mating sexual traits in insects. Several studies have demonstrated that heat stress adversely affects adult mating parameters. For instance, high developmental temperatures have been shown to reduce male mating success, while exposure to heatwaves during the adult stage has increased the time before the first successful mating and decreased mating frequency [17, 38-40]. For example, it was found that high developmental temperatures reduced male mating success [39]. The observations revealed that females accepted the droplet 75.0% of the time when offered by a control male, but only 35.8% of the time with a heat-stressed male. The mating occurrence was significantly lower for heat-stressed males (44%) compared to control males in *Drosophila subobscura* (97%) [41]. When, *Neoseiulus barkeri*, predatory mites were exposed to 42 ºC for 4 hours, males exposed to heat also showed a prolonged copulation duration. A trade-off between survival and reproduction was noted in heat-stressed females [42].

The gonadosomatic index (GSI) for females and sperm count for males are vital for insect fitness and population dynamics. Thermal stress at 45

°C markedly reduced the GSI of *S. frugiperda* in the F_0 generation, with this effect extending into the next two generations but improving somewhat over time [23]. Similar stress impacted F. occidentalis ovariole structure [43], inhibited yolk protein synthesis in *D. melanogaster* [44], and affected ovarian development in *Trichogramma carverae*. Reproductive output trade-offs with thermotolerance under sub-lethal temperatures likely caused these issues [23]. In response to the negative impact of heat stress on insect fertility, insects have adapted their reproductive physiology. These adaptations include pre-copulatory changes that enhance fertility, possibly by improving male mating abilities through increased metabolic activity at higher temperatures [45-46]. Additionally, female mating behaviour has evolved, with a rise in polyandry potentially helping to mitigate fertility declines. For example, females may be more likely to remate after encountering sterile males affected by heat stress [47]. These physiological and behavioural changes represent a strategy to maintain reproductive success under challenging environmental conditions.

4. ROLE OF BIOCHEMICAL CONSTITUENTS DURING HEAT STRESS

The ability of insects to endure heat stress involves complex biochemical processes with neural and sensory hormones, aiding their adaptation to warmer. Their nutrient intake influences their habitat choices at varying temperatures. For instance, *Locusta migratoria* L. lacking carbohydrates prefers cooler settings up to 32 °C, while protein-deficient ones seek warmer areas up to 38 °C environments 6). Additionally, insects build shelters to manage heat stress, light exposure, predators, and bodily functions. The sugar levels in insects are crucial during heat stress. Heat-induced denaturation in insects is mitigated by the production and stabilization of heat shock proteins (HSPs). For instance, during short-term heat stress, the egg and larval stages of insects increase sugar production to counteract heat shock [48]. Exposure to heat stress elevates trehalose and glucose levels in female *Drosophila melanogaster*. Repeated mild heat stress daily enhances dopamine-dependent arylalkylamine N-acetyltransferase activity [49]. Both short-term and long-term heat exposure reduces water and lipid levels but increases glycogen and glycerol in adult *Ophraella communa*, with a notable rise in total sugar content observed after brief thermal stress during egg and larval stages [50]. Consistent with earlier research, insect sugar consumption increases in mosquito, *Aedes aegypti* with temperatures between 20 °C and 30 °C [51]. Studies show that short-term heat stress raises trehalose and glucose levels in female *Drosophila melanogaster* within 30 minutes [52]. This aligns with previous findings that trehalose enhances temperature stress resistance in *Rhyzopertha dominica* larvae [53]. In *D. melanogaster* adults, total lipid content changes after 24 hours of heat exposure. The rapid increase in trehalose and glucose is likely due to heightened synthesis, while the lipid decrease observed after 24 hours may result from reduced food intake during that time [52].

The research examined the impact of elevated temperatures on the protein content, antioxidant enzyme activities, and overall antioxidant capacity (T-AOC) in *Tetranychus urticae* showed that higher temperatures notably increased protein content, antioxidant enzyme activities, and T-AOC, indicating that these enzymes help the mites tolerate heat within the 36–42 °C range [54]. Similarly, heat stress impacted silk production in *Bombyx mori*, with proteins like adenosine kinase (ADK) involved in silk metabolism [55]. For *T. urticae*, protein levels varied significantly with temperature and exposure duration, with higher temperatures (36, 39, 42, and 42 °C) showing increased protein content compared to controls [54]. In *Drosophila*, the protein HSP68 was linked to responses under 39 °C heat stress [56].

Studies show that insects such as *Bemisia argentifolii*, *Corythuca ciliata* and *Plodia interpunctella* typically store sugars and polyols, which help them manage thermal stress. Firefly families have specialized methods for energy storage, while gadflies adapt by having unpredictable reproductive cycles [23]. Insects use glycogen in their fat bodies to mitigate heat damage by regulating the release of sugars and polyols [3] and to provide metabolic water in arid conditions [57]. Studies on *S. litura* [58] and *Bactrocera zonata* [59] reveal that lipid accumulation helps them cope with heat and dryness. Excessive protein production under stress has been noted in Madagascar cockroaches, *Gromphadorhina coquereliana* [60] and green peach aphids, *Myzus persicae*) [61].

It was also noted that a decrease in metabolite accumulation over generations was associated with higher fecundity and shorter lifespan in *S. frugiperda*. Building on earlier research, these

findings highlight the importance of total sugars, glycogen, lipids, and proteins in reducing thermal stress and improving survival and reproductive traits in *S. frugiperda*. Metabolic energy reserves, such as proteins, lipids, and carbohydrates, are essential for insect development [23]. For example, proteins, lipids, and carbohydrates are critical components in insect eggs [62], lipoproteins are necessary in spermatophores [63], and lipids are vital in oocytes [64]. While these nutrient reserves generally support survival and reproduction, they also act as a physiological strategy to withstand environmental stresses, like temperature fluctuations, thereby enhancing insect fecundity and longevity.

5. ROLE OF ANTIOXIDANT ENZYMES DURING HEAT STRESS

Heat stress can cause oxidative harm and stress to the cells, which involves high levels of reactive oxygen species (ROS) inside cells that can harm lipids, proteins and DNA. To prevent ROS damage, antioxidant enzymes play a role in the oxidative harm response. But heat stress can upset this balance and cause more ROS to form, leading to LPO by disrupting cell lipids [65]. Insects utilize key antioxidant enzymes: superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and glutathione S-transferases (GSTs). SOD converts superoxide anions into oxygen and hydrogen peroxide, while CAT and POD decompose hydrogen peroxide [66]. GST eliminates harmful products from lipid peroxidation, indicating oxidative stress and cellular defence [67]. Research has shown that antioxidant enzymes become more active to counteract reactive oxygen species (ROS), protecting insects and mites from heat stress [54].

Studies on *Mythimna separata* revealed that antioxidant enzymes such as SOD, CAT, POX, GST, and the total antioxidant capacity (T-AOC) work together to reduce oxidative stress caused by high reactive oxygen species (ROS) levels in cells when exposed to various thermal stress conditions [68]. Exposure to 35°C and 40°C significantly increased H_2O2 levels in bivoltine and polyvoltine silkworms. Elevated malondialdehyde (MDA) levels, indicating lipid peroxidation, were observed only in bivoltine silkworms. Both silkworm types showed increased antioxidant enzyme activity (CAT, SOD, APOX) under high temperatures, with breed-specific responses to oxidative stress in Bombyx mori [69]. In the carob moth, *Ectomyelois ceratoniae*, the activity levels of two antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT), increased in response to various stressors. This indicates that these enzymes played a protective role for the insects against the effects of heat, cold, starvation, and parasitism by *Habroacon hebetor* wasps [70]. Heat stress on *Liposcelis bostrychophila* led to a significant increase in SOD, CAT, and GST activities but decreased POD activity indicating that different antioxidant enzymes contribute to defence mechanisms and counteract oxidative damage at varying levels [65].

6. ROLE OF HEAT SHOCK PROTEINS DURING HEAT STRESS

Recent breakthroughs in molecular biology and genomics have unveiled a complex network of genes and pathways responsible for insect thermoregulation. A crucial component of this system is the heat shock response, which is regulated by a group of proteins known as heat shock proteins (HSPs) [71]. These chaperone proteins play a vital role in stabilizing cellular structures and preventing protein denaturation during heat stress [72]. The expression of HSP genes is precisely controlled by heat shock transcription factors (HSFs), which bind to specific DNA sequences called heat shock elements (HSEs) in the promoter regions of target genes [73]. HSPs, highly conserved across species, are produced by cells in response to various stressors such as extreme heat, toxins, or UV radiation [74]. They are essential for DNA repair, embryo development, and other critical processes. Among the five major HSP families *viz.,* small HSPs, HSP60s, HSP70s, HSP90s, and HSP110. the HSP70s are particularly responsive to heat and have remained functionally conserved throughout evolution, potentially inhibiting cell death by interfering with apoptotic signals [75]. Heat shock proteins (HSPs) were initially identified in cells subjected to elevated temperatures. These proteins are predominantly expressed in response to various stressors, such as hyperthermia, oxidative stress, heavy metals, inflammation, and infections [76]. Beyond stress response, HSPs play crucial roles in maintaining cellular functions under normal conditions. They are involved in oogenesis, spermatogenesis, and are expressed in both the embryo and maternal decidua during early pregnancy [77]. In mosquitoes, exposure to heat stress triggers a heat shock response, mediated by HSPs like

hsp70, hsp26, and hsp83, which helps mitigate the negative impacts on their physiology, fitness, and survival [6].

During research progresses the role of Hsps are confirmed by Quantitative RT-PCR that heat shock proteins (HSPs) play a crucial role in thermal tolerance, with up-regulation of HSP70 and HSP90 being associated with resilience to both heat and cold. Specifically, HSP70 levels increase more significantly during cold exposure, while HSP90 levels are more responsive to heat [78]. Disrupting HSP70 or HSP90 via RNA interference (RNAi) compromises thermotolerance in larvae of *Plutella xylostella* [79]. Starvation and wasp parasitism also lead to different patterns of HSP gene expression: starvation triggers a higher increase in HSP90, whereas parasitism predominantly up-regulates HSP70 within the first 48 hours while working on *E. ceratoniae* proving that the stress-specific induction of HSPs and highlight the role of antioxidant enzymes in mitigating oxidative stress [70]. In psocids, *Liposcelis bostrychophila* five LbHsps (four LbHsp70s and one LbHsp110) were identified, with most highly expressed in fourth instar nymphs and adults, except LbHsp70-1, which is likely a cognate HSP due to its stable expression [65]. These genes are essential for thermal stress tolerance. RNA sequencing of *Pteromalus puparum* at 25°C and 35°C revealed distinct transcriptional responses, identifying a gene network with two subgroups: one linked to acute heat stress and the other to chronic heat stress and the Xap5 Heat Shock Regulator (XHSR) gene, crucial for lifespan and stress response, was validated through RNA interference and quantitative PCR [80]. Mild heat stress (38°C for 6 hours) in oriental fruit moth, *Grapholita molesta* pupae resulted in transient upregulation of six heat shock proteins (Hsps: 90, 70, 60, 40, 21, and 11) from pupal to adult stages, enhancing adult fitness by improving fecundity and lifespan [81].

Although the upregulation of heat shock proteins (HSPs) is temporary and extends into early adulthood, it positively impacts adult fitness. Some insects experience increased fitness from higher chaperone gene expression after mild stress, leading to greater fecundity and longer lifespan as a carry-over effect. This suggests that mild thermal stress can alter gene expression, enhancing adult fitness through a cascade effect. Insects employ various physiological mechanisms to cope with high temperatures, sensing environmental changes and acclimating accordingly. Initially, sensorial mechanisms involving neurons and neurotransmitters detect environmental signals, triggering responses like metabolic rate adjustments and anaerobic metabolism use.

Table 1. The brief role of heat shock proteins in insect thermoregulation

Sl. No.	Heat shock proteins (HSPs)	Function	References
1.	small HSPs	1. DmHsp27 involved in putative role of molecular chaperone and nuclear processes like chromatin remodeling and transcription. Ex. *Drosophila melanogaster* 2. SmHsp17.4 and SmHsp20.3 are crucial for adapting to heat and cold, and SmHsp17.4, regulated by 20E, is also likely involved in ending diapause, as seen in *Sitodiplosis mosellana.*	82 83
2.	HSP60	1. During oogenesis, HSP62 expression was found dynamic indicating its possible role in oocyte development. Ex. *Lucilia cuprina* 2. Play vital role in degradation of mitochondrial transcription factor A (TFAM), thereby decreasing mitochondrial activity or biogenesis under oxidative stress during diapause. Ex. *Helicoverpa armigera, Bombyx mori*	84, 12
3.	HSP70	1. Potentially involved in the stress and immune responses. Ex. *Musca domestica* 2. Play indispensable roles in the nymphal development, oogenesis and female fertility. Ex. *Nilaparvata lugens*	11
4.	HSP90	Play essential role in nymph development and oogenesis under physiological conditions. Also required during the early developmental stage and played a crucial role in oogenesis, fecundity and late embryogenesis. Ex. *Nilaparvata lugens*	11

7. ROLE OF INSECT NEURONS DURING HEAT STRESS

The nervous system is vital in sensing temperature and triggering appropriate physiological and behavioural responses to high temperatures in animals [85]. Insects display diverse nervous responses to elevated temperatures, influenced by species, populations, and even individuals within the same species, shaped by ecological factors, habitat preferences, and life stages [86]. The necessity of surviving high temperatures drives the natural selection of neural mechanisms involved in temperature detection and response [3]. The heat response in insects begins with thermoreceptor neurons in the peripheral nervous system, which transmit signals to the central nervous system, influencing behaviours such as thermotaxis, heat avoidance, temperature preference, and thermal memory [87]. Thermosensitivity varies widely among insects; for example, antennal neurons of *Drosophila melanogaster* can detect temperature changes as slight as 0.5 °C [88], while leaf-cutting ants (*Atta vollenweideri*) can detect changes as small as 0.005 °C [89]. Thermoreceptor neurons generate action potentials in response to temperature-driven ion concentration changes, leading to chemical messenger release. Most insects, such as cockroaches, locusts, and bees, possess primarily cold receptors, aiding in temperature change detection [6].

Cold receptors are considered to be evolutionarily ancient, while warm receptors likely emerged in smaller dipterans as an adaptation to evade harmful heat [3]. Understanding the influence of body size on the evolution of warm receptors in insect antennae requires further investigation into heat responses across different insect orders. Phylogenetic studies should also explore whether specific neural responses were favoured during periods of historical global warming, and whether insects with warm receptors are better equipped to adapt to rising temperatures due to their enhanced heat detection capabilities. Thermoreceptor neurons are classified into four types: those detecting moderate warmth, intense warmth, moderate cold, and intense cold [90]. In *Drosophila melanogaster*, three types of temperature receptors are present, though cold receptors are lacking. AC neurons in the head detect warmth above 25°C via Transient receptor potential (TRP) channels, while HC neurons in the arista uses gustatory receptors (Gr). These receptors help the fly avoid temperature increases, though this may differ in other insects [91].

Temperature changes influence ion movement across neuronal membranes, leading to the release of neurotransmitters, neuromodulators, and neurohormones like biogenic amines, amino acids, and peptides [92]. These chemical signals enable communication between neurons. Thermoreceptor neurons connect with thermal projector neurons, which target the protocerebrum, lateral horn, and mushroom bodies, allowing the brain to detect environmental temperature and initiate appropriate physiological and behavioural responses [93]. High temperatures trigger a stress response involving heat shock proteins, biogenic amines, and neuroendocrine factors to protect the nervous system and other organs [14]. Elevated temperatures also increase insect metabolism, potentially leading to smaller body sizes over time [94]. Additionally, high temperatures raise levels of juvenile hormone and 20-hydroxy-ecdysone in the haemolymph, which are crucial for regulating diapause and various behavioural and metabolic processes [3]. Insects regulate their body temperature by adjusting flight muscle activity, increasing water loss through spiracles, changing cuticle colour, or altering their activity patterns [95]. In extreme heat, they may enter a reversible heat coma, controlled by neurons in the metathoracic ganglion, to prevent energy loss and manage gas exchange through the tracheal system. This coma prevents neural and muscular system damage, similar to cortical spreading depression in vertebrates, and is marked by elevated extracellular K^+ levels and electrical silence in the central nervous system [96]. The genetic basis for heat coma protection in *Drosophila melanogaster* involves the foraging gene, which encodes cyclic GMP (cGMP)-dependent protein kinase (PKG). This gene helps protect against thermal stress by regulating Ca^{2+} flow in synapses [97]. In *Locusta migratoria*, adapted to high temperatures, the ventilatory central pattern generator (vCPG) in the metathoracic ganglion manages oxygen and carbon dioxide levels [3]. During heat coma, this system enhances heat loss through evaporation, maintaining a lower body temperature. Pre-stress shields the vCPG from hyperthermia, a response that can be replicated with serotonin, highlighting the role of this neurotransmitter in temperature adaptation.

8. ROLE OF INSECT HORMONES DURING HEAT STRESS

Insects are the most diverse group of animals, thriving in a wide range of habitats, including extreme environments like deserts and polar regions. Their remarkable survival skills stem from their ability to withstand environmental stresses, particularly freezing temperatures [98]. The neuroendocrine system, involving neuropeptides and biogenic amines, plays a key role in managing these physiological changes, enhancing cold tolerance [92]. The neuroendocrine system and various signalling molecules, like CAPA, Ion transport peptide (ITP), and Transient receptor potential (TRPs), contribute to cold stress adaptation of insects. It has been already found that the oxidative stress induced by different stressors, monitored through specific biomarkers, and details adipokinetic hormones (AKH) role in mitigating these effects. AKH levels rise significantly in response to stress, helping to reverse stress-induced disruptions. The proposed mechanism involves protein kinase C, cyclic AMP pathways, and Ca^{2+} stores, with potential involvement of FoxO transcription factors. Other roles of insect hormones in anti-oxidative defence are also explored [99]. Hormones are vital in regulating physiological responses of insects under extreme conditions like high temperatures [92]. Diapause, a period of suspended development, helps insects survive harsh environments such as heat and drought, involving complex gene modules rather than a single gene [100]. During diapause, the endocrine system manages adaptations like halted development, fat storage, and reduced metabolism [101].

Temperature affects hormone biosynthesis significantly, particularly juvenile hormone (JH) and 20-hydroxy-ecdysone (20E), which influence life-history traits [102]. Juvenile hormone (JH) and 20-hydroxyecdysone (20E) are crucial in the neuroendocrine stress response, influencing alkaline phosphatase activity, which in turn regulates biogenic amines like octopamine (OA), a key player in thermal tolerance [13]. High temperatures prompt a rapid increase in OA levels in these flies, subsequently elevating JH and 20E levels, which affects female fecundity [103]. Considering the role of JH in regulating life-history traits, its involvement in balancing heat tolerance with other traits requires further study. The stress response in insects, like in vertebrates, begins with the quick release of biogenic amines. These amines regulate various physiological processes, and their increased levels during heat stress, as seen in *Locusta migratoria*, enhance heat tolerance [92].

9. ROLE OF CUTICULAR PROTEINS DURING HEAT STRESS

The insect cuticle plays a vital role in maintaining the insect's body shape, preventing dehydration, and defending against microbial infections. Water loss in insects is associated with changes in the amount and composition of cuticular lipids, as noted in several studies [104]. Temperature fluctuations can influence the structure of these lipids, highlighting their importance in temperature adaptation. To cope with varying temperatures, insects adjust their cuticular lipid levels [105]. Cuticular hydrocarbons are crucial for recognizing mating signals, conserving water, and ensuring waterproofing [106]. The insect cuticle is primarily composed of chitin, proteins, and lipids. Insect cuticular proteins (CPs), classified into over 12 families based on their amino acid sequences, exhibit varied expression patterns according to developmental stages and tissue types [11]. While CP production increases under heat stress, the specific role of these proteins in heat acclimation remains unclear [107]. To investigate the role of CP genes in heat acclimation, researchers found that heat-acclimated larvae had higher heat tolerance and increased cuticular protein content compared to unacclimated larvae. They identified 191 potential CP genes in *Cnaphalocrosis medinalis*, with 14 showing different expression patterns under heat stress. RNAi experiments revealed that CmTweedle1 and CmCPG1 are involved in heat acclimation, affecting both heat tolerance and cuticular protein content [104].

10. CONCLUSION

Overall, there is a complicated network of genes that are involved in thermoregulation for insects indicating the significance of various physiological mechanisms within them. Heat shock proteins mainly act by protecting the cell's integrity. Besides, it entails signs that heat stress circumstances make the reproductive processes more fragile. The development and stress responses of insects are changeable based on hormones secreted by them while their enzyme antioxidants can reduce oxidizing agents' effects. Moreover, cuticular proteins help sustain their shape, and carbohydrates-proteins breakdown provides the body power needed during high temperature. These molecular and physiological

adaptations not only extend our comprehension of insect endurance under environmental alterations but also present important guidelines for pest control as well as biological group protection from global warming.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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