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Review article

Response mechanisms to heat stress in bees

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Abstract – Bees are vitally important in natural and agricultural ecosystems, providing key pollination services to wild plants and crops. Increasing reports of regional declines of bee populations have attracted intense attention worldwide. Challenges to bee health are multifactorial and include poor nutrition, heat stress, agrochemicals, and pathogens. The impact of heat stress is a relatively minor factor in current bee declines compared with agrochemicals and pathogens. However, heat stress has adverse impacts on foraging activity, pollination services, task-related physiology, immunocompetence, reproductive capacity, growth, and development of bees, and these adverse impacts are variable in different bee species. Heat stress–related damage to bees receives extra attention when it is accompanied by climate change. Heat-tolerance mechanisms are key enablers for bee survival under high-temperature stress conditions, and we now understand that both behavior and molecular regulation strongly impact the ability of bees to reduce damage from heat stress. In this review, we summarize and synthesize previous findings about the detrimental effects of heat stress to bees and discuss the strategies bees use to cope with heat stress. Bee species mentioned here are mainly honeybees, bumblebees, and stingless bees, with a focus on the honeybee *Apis mellifera* .

bees / population decline / heat stress / climate change / defense strategies

1. INTRODUCTION

Pollinators are essential in mediating the exchange of pollen between cultivated and wild plants, facilitating seed and fruit production (Vasiliev and Greenwood 2020; Zou et al. 2017; Benjamin and Winfree 2014). It is estimated that 87.5% of wild-flowing plants benefit from insect pollinators, with 20% of these benefiting from bees (Ashman et al. 2004; Ollerton, 2017). However, severe regional losses of some wild bee populations and honeybee colonies (*Apis mellifera*) have been frequently reported worldwide over the past decade (Campos 1998; Goulson et al. 2015; Soroye et al. 2020). Bee declines have had negative economic and ecological effects, and it is anticipated that these declines represent a real threat to the maintenance of crop production, natural ecosystems stability, human welfare, and plant diversity (Potts et al. 2010; Powney et al. 2019; Soroye et al. 2020; Theisen-Jones and Bienefeld 2016; Vanengelsdorp et al. 2009). Known drivers of these declines include pathogens, agrochemicals, habitat loss, alien species, and heat stress (Evans and Schwarz 2011; Goulson et al. 2015; Lopez-Uribe et al. 2020; Nicholson and Egan 2020).

Among these factors, heat stress affects pollination services and foraging activity, as well as the growth and development of bees; the impacts may be not exactly the same in different bee

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species (Alqarni 2020; Bordier et al. 2017b; Greenop et al. 2020; Rasmont et al. 2015; Souza-Junior et al. 2020). These adverse impacts can become more obvious with climate change, with especially evident changes occurring in the tropics, cold regions, and mountains (Alqarni 2020; Deutsch et al. 2008; Kerr et al. 2015; Medina et al. 2018; Rasmont et al. 2015; Soroye et al. 2020). This is because an increase in the intensity and duration of heat waves is a key aspect of climate change (Mora et al. 2017; Xu et al. 2018): the temperatures of tropical areas are already warm, and any increases in temperature caused by climate change will possibly be more deleterious in the tropics than in temperate regions (Deutsch et al. 2008; Mora et al. 2013).

It is worth noting that climate change is apparently happening faster than initially predicted (Xu et al. 2018). Even so, many studies have revealed that bees are using some behavioral and physiological strategies to survive better under heat stress (Bonoan et al. 2014; Johnson 2002; Siegel et al. 2005). Changes in the expression of some genes, such as the nuclear factor Y (NF-Y) and heat shock protein (Hsp) families (Li et al. 2020a, b; Liu et al. 2012; Liu et al. 2014; McAfee et al. 2020b; Zhang et al. 2014), have also been observed in response to heat stress. Here, we summarize the existing knowledge about the adverse effects of heat stress on bee colonies, such as honeybees (especially *A. mellifera*), bumblebees, and stingless bees, and we present known information about defense mechanisms that bees use to manage heat stress. It is worth mentioning that the impacts of heat stress on bees and the defense mechanisms of bees to heat stress are variable in different bee species or subspecies.

2. THE EFFECT OF SPECIES AND BODY SIZE ON BEE TOLERANCE TO HEAT

Differences in heat resistance capacity have been found across different bee species. In the Arabian Peninsula, the longevity of *A. mellifera carnica* is significantly lower compared with *A. mellifera jemenitica* at an ambient temperature of 40 °C (Abou-Shaara et al. 2012). The thermal limits and metabolic rates of *A. mellifera ligustica* are more tolerant to high temperature than *A. mellifera carnica* (Kovac et al. 2014). In hot-arid subtropical ecosystems, native *A. mellifera jemenitica* foragers are more heat resistant (with the lowest *Hsp* expression level) compared with imported European *A. mellifera carnica* and *A. mellifera ligustica* (Alqarni et al. 2019). Under semiarid and desert climates, colony losses are significantly higher in exotic bee subspecies *A. mellifera ligustica* (84%) and *A. mellifera carnica* (92%) than that in the indigenous bee *A. mellifera jemenitica* (46%), and most of bee colony losses happen in summer months, such as August and September (Alattal and Alghamdi 2015). In addition, *A. cerana* displays a lower survival rate and reduced body water loss at 40 °C and 45 °C compared with *A. mellifera*, and *A. cerana* is mostly intolerant at 57–60 °C, while *A. mellifera* is intolerant at 54–60 °C, yet *A. cerana* has been shown to have a higher water loss rate than *A. mellifera* under extremely high temperatures (Li et al. 2019). These results indicate that *A. mellifera* is apparently more tolerant than *A. cerana* under high temperatures, whereas *A. cerana* is more tolerant than *A. mellifera* under extremely high temperature (Li et al. 2019).

The difference of heat resistance in different bumblebee species is also presented (Martinet et al. 2015; Oyen et al. 2016; Zambra et al. 2020). The heat resistance threshold temperature of high-elevation species (*Bombus sylvicola* and *B. bifarius*) is nearly 5 °C lower than for low-elevation species (*B. huntii*) (Oyen et al. 2016). High-elevation species (*B. alpinus* and *B. balteatus*) are less tolerant to heat stress than species from low elevations and latitudes (*B. monticola*) (Martinet et al. 2015). Moreover, the time before heat stupor of the males of the most widespread bumblebee species *B. lucorum* and *B. terrestris* is longer than that of declining bumblebee species such as *B. magnus* and *B. jonellus*, indicating that the heat resistance of male *B. lucorum* and *B. terrestris* is higher than in male of *B. magnus* and *B. jonellus* (Zambra et al. 2020), and this difference may influence their survival in the context of climate change. These results indicate that heat resistance of bees is species-specific.

Body size is also known to influence the heat tolerance of bees (Oyen et al. 2016; Pereboom and Biesmeijer 2003). It has been shown that small stingless bees lose heat much more rapidly than larger ones (Pereboom and Biesmeijer 2003), indicating that smaller stingless bees may be more tolerant than larger ones. Another study reported that relatively larger bumblebees can tolerate higher extreme temperatures, which may be due to a thermal-inertia–driven lag for the larger bumblebees between the air temperatures and core body temperatures (Oyen et al. 2016). However, it is also proved that there is no significant connection between body size and the time before heat stupor throughout all specimens based on linear models in bumblebees (Zambra et al. 2020). This apparent discrepancy in whether body size affects the heat resistance of stingless bees or bumblebees suggests a fruitful area for future investigations.

3. DETRIMENTAL IMPACTS OF HEAT STRESS ON BEES

The adverse effects of heat stress on bees include multiple aspects such as their growth, development, task-related physiology, immunocompetence, foraging activity, pollination services, and reproduction (Alqarni 2020; Bordier et al. 2017b; Greenop et al. 2020; Medina et al. 2018). Heat stress can trigger malformations of the proboscis, stinger, wings, and legs in *A. mellifera carnica* (Groh et al. 2004). Besides, when Africanized *A. mellifera* pupae are reared at 40 °C for 1 h daily across 6 days, the resultant adult bees are slightly shorter than adults raised at normal colony temperatures, and the heat-exposed adults have obviously increased fluctuating asymmetry in forewing shape, reduced longevity, and decreased age at the onset of foraging (Medina et al. 2018). There are also reports from *A. mellifera* that exposure to high temperatures during development induces precocious age at onset of foraging, causes bees to dance for longer periods and dance more often as adults, and affects synaptic organization and memory (Becher et al. 2009; Groh et al. 2004; Tautz et al. 2003). These results indicate that heat stress has adverse effects on *A. mellifera* growth and development. Heat stress also decreases bumblebee colony development, causing lower investment in offspring production, and small colonies are known to be more sensitive to heat change than the relatively larger colonies (Vanderplanck et al. 2019). Notably, the impacts of heat on small colonies are far less pronounced after feeding with suitable diets, indicating that suitable diets decrease the effects of heat stress to bumblebees (Vanderplanck et al. 2019).

In addition to impacts on growth and development, heat challenge influences bee task–related physiology and immunocompetence in *A. mellifera* (Bordier et al. 2017b; Medina et al. 2020). Heat stress induces the expression of vitellogenin (*vg*) and juvenile hormone esterase (*jhe*) in *A. mellifera* foragers (Bordier et al. 2017b). Previous research found that *vg* and *jhe* are associated with the regulation of task specialization and typically have low expression levels in foragers (Robinson 1987); foragers have lower levels of *vg* and *jhe* than nurses (Bordier et al. 2017b). Therefore, heat-stressed bees that tend to express a nurse-like profile for brood thermoregulation may be triggered by heat-related increases in the expression levels of *vg* and *jhe* (Bordier et al. 2017b). Moreover, heat stress during development influences the immunocompetence in drones, workers and queens of Africanized *A. mellifera*, and heat-stressed workers exhibit significantly decreased longevity after infection with *Metarhizium anisopliae* (Medina et al. 2020).

Impacts of heat on bee foraging activity and pollination services have also been reported. For example, in the middle of a desert, pollen-gathering and foraging activities are negatively influenced by temperature, and bees decrease pollen-gathering and foraging activities during hot-dry-windy weather in *A. mellifera*. However, hive location in nectar-rich Acacia trees decreases the negative impacts of hot-dry-windy weather to *A. mellifera* foraging activity (Alqarni 2020), which indicate that providing high-quality diets and sufficient sources of nectar may help to maintain the foraging activity of *A. mellifera* under heat stress. Bean plants pollinated by heat-stressed bumblebees have lower total bean weight and proportional pod set compared with those pollinated by non-heat-stressed bumblebees (Greenop et al. 2020). Increasing heat on stingless bee foragers (*Melipona subnitida*) results in increased flight distance in a Brazilian tropical dry forest (Souza-Junior et al. 2020), which may finally result in an overall decrease in the foraging activity and pollination services of stingless bees.

Furthermore, heat stress affects animal reproduction through influencing factors such as sperm quality (Hurley et al. 2018; Sales et al. 2018). Heatwaves decrease sperm competitiveness, ejaculate sperm number, and male fertility in *Tribolium castaneum* (Sales et al. 2018). The impact of heat stress on *A. mellifera* sperm has also been reported. The availability of stored sperm in the *A. mellifera* queen is significantly reduced under heat stress (Pettis et al. 2016). Furthermore, *A. mellifera* males die after exposure to 40 °C for 24 h, and the viability of ejaculated sperm is decreased after heat stress (Stürup et al. 2013). Temperatures from 15 to 38 °C are safe for *A. mellifera* queens at a tolerance threshold of 11.5% loss of sperm viability, and heat stress induces the expression levels of some stress-related proteins in the spermatheca (McAfee et al. 2020a). Despite these findings, the effects of heat stress on bee queen reproduction and drone sperm quality still need further study.

4. STRATEGIES USED BY BEES TO DEFEND AGAINST HEAT STRESS

Heat stress can happen at the whole-colony level and significantly influence the growth and development of larvae, pupae, and nurse adults (Bonoan et al. 2014; Medina et al. 2018). Moreover, heat stress can occur at the individual level of foragers when they are collecting pollen and nectar in the environment (Souza-Junior et al. 2020). To better survive under heat stress, bees have deployed some compensatory strategies at the behavioral and molecular levels to defend against heat stress (Figure 1) (Bonoan et al. 2014; Heinrich 1976).

4.1. Behavioral levels

4.1.1. Decreasing hive temperature

The temperature of beehives is strictly regulated at the colony level for normal colony function and brood development. For example, the temperature of honeybee, bumblebee, and stingless bee hives is carefully maintained between 32 and 36 °C (Jones et al. 2004; Seeley 1985), 28-32°C (Vogt 1986), and 26-30°C (Marques et al. 2020), respectively. When a hive temperature is above the thermal optimum, a series of behaviors are used by the bees in the colony to actively regulate the hive temperature and maintain normal brood temperatures (Figure 1a). The following is mainly focused on the behaviors of honeybees (*A. mellifera*) in reducing hive temperature. The behaviors of bumblebee and stingless bees in regulating their hive temperature still need further research.

To reduce hive temperature, an increase in water collecting foragers is found in *A. mellifera* (Bordier et al. 2017a), and workers fan their wings when standing at the hive entrance, or fan their wings in the hive; honeybees may also simultaneously hold a thin film of water in their proboscis to achieve evaporative cooling (Heinrich 1980; Southwick and Heldmaier, 1987; Wilson 1971). Moreover, many honeybees will vacate the hive and cluster outside the hive entrance when cooling measures are insufficient. A sufficient number of bees is retained within the nest to continue activity supporting evaporation and ventilation (Southwick and Heldmaier, 1987). If all of these behavioral measures are insufficient as a response to heat stress, further reallocation of labor will occur: the additional labor needed for the heat stress response of a hive is acquired by reallocating middle-aged bees away from their current tasks (Johnson 2002).

Furthermore, honeybee workers can use asocial homeostatic heat-shielding behavior to defend against excessive local heat changes in hives (Bonoan et al. 2014; Starks and Gilley 1999; Starks et al. 2005). Specifically, young workers have been observed to act as a heat shield by placing their ventral surface against a potentially over-heated brood comb or orienting their ventral side directly against a heated surface to achieve heat shielding, passively absorbing heat by establishing a physical barrier (Siegel et al. 2005; Starks and Gilley 1999; Starks et al. 2005). Upon absorbing heat, the next step of a heat-shielding worker is to dissipate this heat. At least two mechanisms for heat dissipation have been reported: pattern-rich dissipation and pattern-free dissipation (Bonoan et al. 2014). Pattern-rich heat dissipation is characterized by a directed trend of movement for the heated workers away from the

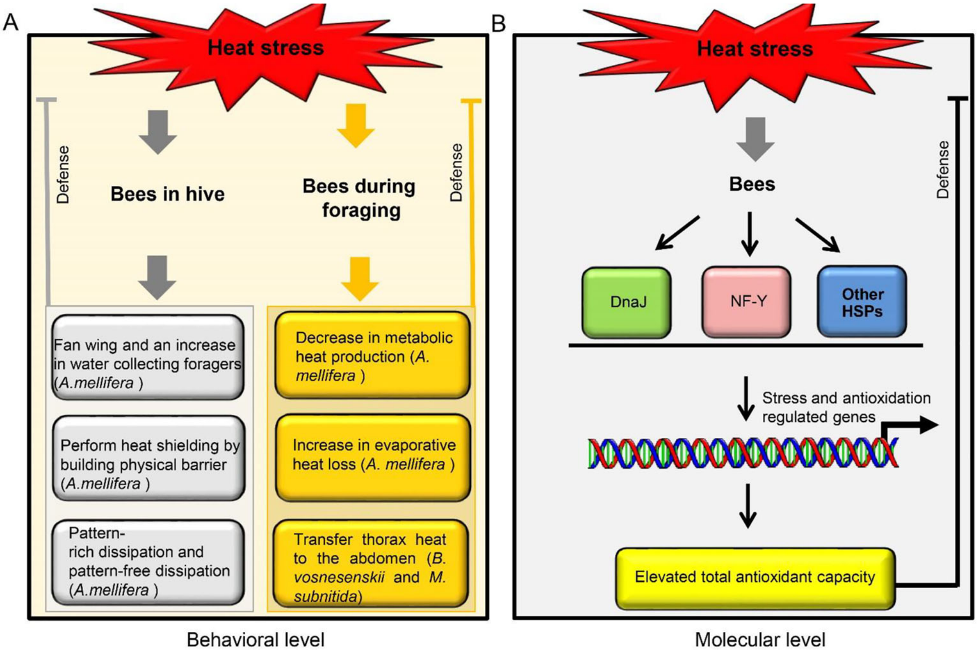

Figure 1. The defense strategies of bees to heat stress at the behavioral level (**a**) and the molecular level (**b**). **a** Defense strategies at the behavioral level under heat stress. When the temperature of *Apis mellifera* hive exceeds the normal optimum temperature range, workers can fan their wings, perform heat-shielding behavior to passively absorb heat, dissipate heat through pattern-rich dissipation and pattern-free dissipation manners, and increase in water-collecting foragers. When foragers suffer from heat stress during foraging, they present decrease in metabolic heat production and increase in evaporative heat loss (*A. mellifera*) and can transfer thorax heat to the abdomen (*Bombus vosnesenskii* and *Melipona subnitida*). **b** Defense strategies at the molecular level under heat stress. Heat stress induces the expression of some members of heat shock protein (*Hsp*) and nuclear factor Y (*NF-Y*) gene families. The accumulation of Hsp and NF-Y will promote the transcription of many heat-inducible genes and antioxidant genes, which contributes to elevating the antioxidant capacity of bees and supports increased defense against heat stress

heated region of a hive to other hive areas such as pollen stores and honey, or even out of the hive (Bonoan et al. 2014). With pattern-free heat dissipation, there is no obvious trend in the direction of movement of heated workers within the hive (Bonoan et al. 2014). Workers can effectively reduce the temperature of the brood comb back to safe levels within 10 min (Bonoan et al. 2014).

4.1.2. Reducing heat stress during foraging

Beyond heat stress experienced in a hive, bees also suffer from heat stress during foraging, with especially evident heat-related risk to the thorax of foragers. Thermoregulation of thoracic temperature plays crucial roles in the ability of bees to fly (Heinrich 1976; Roberts and Harrison 1999; Souza-Junior et al. 2020). For example, the thoracic temperature of both honeybees and bumblebees can exceed 40 °C during flight (Heinrich 1976; Kovac et al. 2018). Inappropriate regulation of thoracic temperature will trigger heat stress of bees, particularly for tropical bees for which ambient air temperatures are already high (Souza-Junior et al. 2020).

Bees have developed countermeasures to prevent thorax overheating (Figure 1a) (Bordier et al. 2017a; Roberts and Harrison 1999; Souza-Junior et al. 2020). Heated bumblebees (*B. vosnesenskii*) can prevent overheating of their thorax by transferring thorax heat to the abdomen. Notably, when heart function was made inoperative, this thorax-to-abdomen heat transfer ability was abolished (Heinrich 1976).

In stingless bees (*M. subnitida*) in the Brazilian tropical dry forest, increasing heat stress of the thorax occurs alongside increasing flight distance. When closest to the nest (15 m), foragers increase heat dissipation from the thorax to the abdomen and head with increasing foraging distance to avoid overheated thoracic temperatures. However, when relatively far away from the nest (100 m), *M. subnitida* cannot compensate for the elevated heat gain in the abdomen and head, resulting in temperature changes in these body parts (Souza-Junior et al. 2020). For *M. subnitida* in the Brazilian tropical dry forest to avoid heat stress, foraging close to the nest may be a useful behavior.

Furthermore, in *A. mellifera*, the dominant mechanism of prevention of thorax overheating during flight as air temperature increased from 33 to 45 °C is a decrease in metabolic heat production and an increase in evaporative heat loss (Roberts and Harrison 1999). All these results indicate that behavioral measures function in heat stress management of bees.

4.2. Molecular level

Bees not only respond to heat stress through behavioral changes, they also enhance their heat resistance by gene expression regulation. Under heat stress, bees induce the expression of many key genes and proteins, including Hsp, NF-Y, acetylcholinesterase 1 (AchE1), and zinc finger protein (ZFP) (Figure 1b) (Kim et al. 2019; Li et al. 2020a, b; Ma et al. 2019; Zhang et al. 2014). In addition, heat stress can cause the production of reactive oxygen species (ROS). High levels of ROS will trigger oxidative damage to organisms (Finkel and Holbrook 2000; Slimen et al. 2014). Expression of some genes can reduce ROS content and thereby reduce the oxidative damage caused by heat, which may increase the survival rate of bees under heat stress (Figure 2) (Li et al. 2020a, b).

4.2.1. The role of Hsp in bee responses to heat stress

Hsp are categorized into six classes, including small Hsp (sHsp), Hsp40 (also known as DnaJ), Hsp60, Hsp70, Hsp90, and Hsp100, according to their molecular masses (King and MacRae 2015; Ohama et al. 2017). Among these, Hsp40 is categorized into three subfamilies, including DnaJA, DnaJB, and DnaJC (Craig et al. 2006; Craig and Marszalek 2017; Kampinga and Craig 2010).

Hsp40 subfamily genes (*DnaJA1*, *DnaJB6*, *DnaJB14*, *DnaJC28* and *DnaJ1*) can be quickly induced by heat stress in *A. cerana cerana*, while *DnaJB12* and *DnaJC8* are induced during long-term heat stress in *A. cerana cerana* (Li et al. 2020a). Silencing *DnaJA1*, *DnaJB12*, and *DnaJC8* causes *A. cerana cerana* to be more sensitive to heat, indicating that *DnaJA1*, *DnaJB12*, and *DnaJC8* may serve as positive regulators of heat stress responses (Li et al. 2020a). Heat stress produces ROS, resulting in increased oxidative damage to organisms (Finkel and Holbrook 2000; Slimen et al. 2014). DnaJA1 can regulate the expression of many antioxidant genes and heat stress response genes, thereby improving the antioxidant ability of bees under heat stress (Figure 2) (Li et al. 2020a). In addition, several members of the *sHsp* subfamily (*Hsp22.6*, *Hsp23.0*, *Hsp24.2*, and *Hsp27.6*) also participate in bee heat stress responses (Liu et al. 2012; Liu et al. 2014; Zhang et al. 2014). For example, under heat stress conditions, the transcription of *Hsp22.6* is continually increased in *A. cerana cerana*. Knockdown of *Hsp22.6* significantly reduces the survival of *A. cerana cerana* under heat stress (Zhang et al. 2014), indicating that upregulation of *Hsp22.6* may increase the tolerance of *A. cerana cerana* to heat.

Interestingly, recent studies have compared the expression of *Hsp* in different *A. mellifera* subspecies (Alqarni et al. 2019). When honeybees are exposed to 40 °C, exotic European bee subspecies (*A. mellifera carnica* and *A. mellifera ligustica*) can express *Hsp70*, but the indigenous bee subspecies (*A. mellifera jemenitica*) does not express any *Hsp*. When the temperature is raised to 45 °C, *Hsp40* and *Hsp70* are expressed in *A. mellifera carnica*; *Hsp40*, *Hsp60*, and *Hsp70* are expressed in *A. mellifera ligustica*, whereas *A. mellifera jemenitica* foragers express only one *Hsp* (*Hsp70*) (Alqarni et al. 2019). These results indicate that *A. mellifera jemenitica* foragers may be more tolerant to increased temperatures, with their bodies requiring relatively reduced *Hsp* expression levels to cope with heat stress.

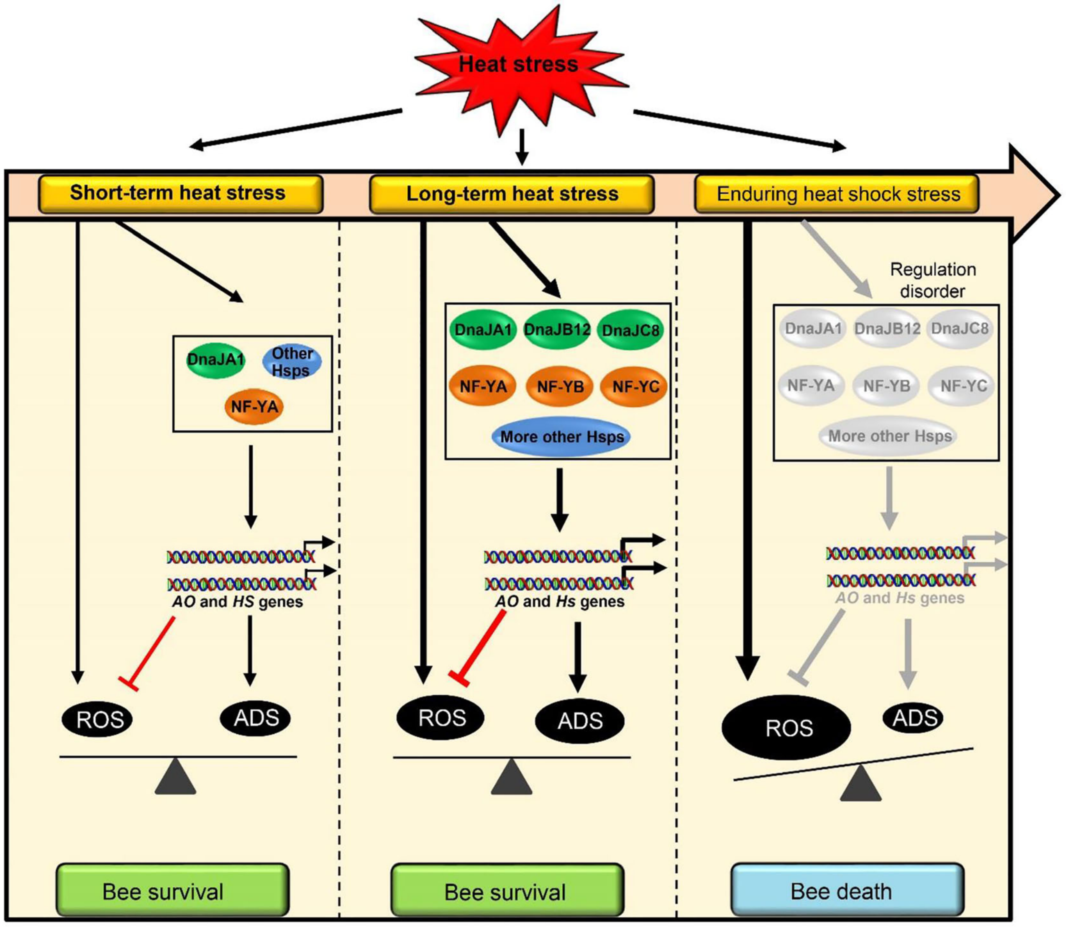

Figure 2. Molecular mechanisms through which bees cope with different degrees of heat stress. Heat stress can induce the production of reactive oxygen species (ROS), high levels of which can trigger oxidative damage to organisms. Short-term heat stress upregulates some heat shock protein (*Hsp*) family (such as DnaJA1) and other types of proteins [such as nuclear factor YA, (NF-Ya)], which can accelerate the expression of many heat-inducible genes (HS) and antioxidant genes (AO), thereby enhancing the antioxidant defense system (ADS), and then help scavenge ROS and reduce the oxidative damage caused by heat stress, contributing to bee survival. Under long-term heat stress conditions, a small number of heat stress regulators are not sufficient for bees to resist heat stress. Under long-term stress, the expression of additional *Hsp* and other gene family members is upregulated, which in turn scavenge ROS, enhance the antioxidant defense system of bees, and increase the survival rate of bees under heat stress. If the duration is increased again, the balance between ROS overproduction and the antioxidant defense system is disordered. Bees cannot bear this degree of heat stress and will die

4.2.2. The functions of other genes in bee heat stress responses

Beyond the *Hsp*, an increasing number of apparently heat stress–related genes have been gradually discovered. For example, the expression levels of *NF-YA*, *NF-YB*, and *NF-YC* are induced under long-term and short-term heat stress in *A. cerana cerana* and *A. mellifera*. In *A. cerana cerana*, knockdown of *NF-YB* and *NF-YC* decreases the antioxidant capacity and increases the oxidative damage caused by heat. Upregulation of *NF-Y* may increase the heat resistance of bees under different heat stress conditions by reducing oxidative damage and enhancing antioxidant ability (Figure 2) (Li et al. 2020b). In addition, a recent study reported that the expression of honeybee *AChE1* is significantly induced by heat stress, and this induction degree is more apparent in the abdomen than in the head (Kim et al. 2019). A recent transcriptome study showed that the mRNA levels of *ZFP* (such as *ZFP271*, *ZFP37*, *ZFP239*, *ZFP776*, and *ZFP93*) and serine/threonine protein kinase (*STK*) (such as *STK-6*) are regulated by high temperatures, indicating that they may function in the response of bees to heat stress (Ma et al. 2019).

5. THE CONNECTION BETWEEN HEAT STRESS AND BIOTIC STRESSES

It is worth mentioning that heat stress in beehive can reduce the infection from viruses and parasites (Palmer-Young et al. 2019; McMenamin et al. 2020; Hoppe and Ritter 1987). For example, high temperature can ameliorate infections of *Crithidia bombi* to bumblebees, without apparent damage to the major symbiont species in bumblebees. The infection intensity of *C. bombi* to bumblebees is reduced by over 80% between 21 and 37 °C (Palmer-Young et al. 2019). In addition, high temperature confers bumblebee tolerance to infection by *Serratia marcescens*, *Klebsiella*, *Erwinia* spp, *Salmonella*, *Yersinia*, and *Escherichia coli* (Palmer-Young et al. 2019). It has also been shown that heat responses can be antiviral in *A. mellifera*: heat-shocked *A. mellifera* (42 °C for 4 h) can decrease levels of a model virus (Sindbis-GFP) compared with bees reared at 32 °C (McMenamin et al. 2020). Deformed wing virus loads are significantly decreased under simulated heat waves in *A. mellifera* (Bordier et al. 2017a). In honeybees, heat is also used to kill *Varroa* by heat honeybee hives (Hoppe and Ritter 1987; Rosenkranz et al. 2010). These results indicate that bumblebees and *A. mellifera* may "benefit" from defending against infection under heat stress to some extent. However, the benefit of heat to defense against infection also incurs costs, because heat stress has adverse effects on immunocompetence, pollination services, task-related physiology, growth, and development of bees (Alqarni 2020; Bordier et al. 2017b; Greenop et al. 2020; Medina et al. 2018).

6. CONCLUSION AND FUTURE DIRECTIONS

Heat stress affects the growth, development, and foraging activity of bees and also increases oxidative damage by promoting ROS generation, thereby threatening the survival of bees (Alqarni 2020; Bordier et al. 2017b; Finkel and Holbrook 2000; Greenop et al. 2020). However, bees also deploy defense systems against excessive ROS content, thereby slowing the oxidative damage caused by heat stress (Figure 2) (Li et al. 2020a, b). With the intensification of climate change, the defense capacity of some bee species may not have been sufficient to maintain adequate adaptation to the environment, which has contributed to large declines in bee populations in many regions (Kerr et al. 2015; Soroye et al. 2020). Therefore, heat-resistance mechanisms should be investigated thoroughly to improve our knowledge about heat-resistance mechanisms of bees.

Although the responses of bee to heat stress have been studied for a long time, many outstanding questions remain. First, bees are often challenged by heat stress along with other stresses, such as pathogens and agrochemicals (Evans and Schwarz 2011; Goulson et al. 2015; Lopez-Uribe et al. 2020). Researchers should continue to identify the mechanisms underlying responses to heat and other stressors in the future. In particular, the discovery of genes that respond to both heat stress and other stresses could indicate that bees may be able to deal with simultaneous environmental stresses. Second, because bees have different tolerances to heat stress at different developmental stages (Alqarni et al. 2019; Jones et al. 2005; Kim et al. 2019), further experiments can explore genes and signal pathways involved in heat resistance at various developmental stages of bees, which may suggest stage-specific–targeted control strategies. Third, although the effect of heat stress on bee behavior is relatively clear (Bonoan et al. 2014; Johnson 2002; Southwick and Heldmaier, 1987), the molecular regulatory networks and neurological components in bees underlying their responses to heat stress still require more study.

Fourth, differences in the defense mechanisms of bees to long-term vs. short-term heat stress and the different tolerance ranges of different castes of bees also need further study. Finally, given that bees can thermoregulate reasonably well of their hive, it will be fruitful to investigate how big the risk of extreme heat events (heatwaves) actually is to colonies and how hot does it have to be before detrimental temperatures actually occur in a colony accompanied by climate change.

AUTHOR CONTRIBUTIONS

Xingqi Guo and Baohua Xu designed the work. Hang Zhao, Xingqi Guo, and Baohua Xu wrote the manuscript, and all the authors approved the final version of the manuscript.

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Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest The authors declare that there are no conflicts of interest.

We declare that the manuscript has not been published previously and is not currently submitted for review to any other journal.

Mécanismes de réponse au stress thermique chez les abeilles.

Abeilles / déclin de la population / stress thermique / changement climatique / stratégies de défense.

Reaktionsmechanismen von Bienen gegenüber Hitzestress.

Bienen / Populationsrückgang / Hitzestress / Klimawandel / Abwehrstrategien

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