

HIVE TEMPERATURE REGULATION BY HONEYBEES IN RESPONSE TO EXTREME CONDITIONS

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ABSTRACT

Honeybees are considered the primary pollinators of agricultural crops. However, climate change, pesticide use, disease transmission and pests all have an impact on their survival. Temperature is an important consideration, especially when bees are subjected to harsh conditions as a result of the effort required to regulate them within their hives. The brood chamber should be kept between 33 and 35 °C. The recognized temperature thresholds are 6 and 38 °C; deviations above or below these values cause metabolic damage in honeybees; the larger the difference, the greater the stress. These eusocial insects have developed thermoregulating mechanisms in response to adverse environmental conditions; the colony compensates for this difference by either fanning their wings to create air circulation and cause evaporative cooling or raising the temperature by generating endothermic heat to raise the temperature of the breeding chamber. This review brings together the most important and updated references on how to improve colony thermoregulation and its relationship to climate change.

Keywords: *Apis mellifera* L., thermoregulation, extreme temperatures.

INTRODUCTION

Honeybees (*Apis mellifera* L.) are the most valuable pollinators in agriculture around the world. However, devastating colony losses have recently occurred due to synergistic factors. Climatic conditions are an important factor in the bee colony's well-being. Within the hive, the brood chamber must be strictly controlled within the range of 33 to 35 °C; maintaining such a narrow range is critical for proper brood development (Eouzan *et al.*, 2019). As a result, if the temperature exceeds this range, bee physiology and behavior are affected.

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Currently, conventional Langstroth chambers are the most popular among beekeepers due to their low cost and ease of operation. They are constructed with softwood from various timber species with a thickness of approximately 23 mm. This design has a deficient isolating factor, which causes an unstable hive microclimate (Mitchell, 2019). This is critical in areas where temperatures reach extreme levels, resulting in declining colony populations, death, and the unexplainable disappearance of colonies. Beekeepers have traditionally suffered from winter losses, but in recent years, summer losses have increased, posing a new threat. Steinhauer *et al.* (2021) studied colony losses in the USA from 2020 to 2021 and discovered losses of up to 32.2 % during the winter and 31.3 % during the summer.

Worldwide colony losses are increasing year after year, which has been linked to global climate change (IPCC, 2023). Although many threats affect the honeybee industry, the occurrence of extreme temperatures is linked to colony losses (Alattal and Alghamdi, 2015). Nonetheless, honeybees have an outstanding capacity to adapt to different environments. Beekeeping is extended worldwide in very different climates, though resilience is somewhat limited. Fast global warming is threatening genetic variability, making it a limiting factor because the accelerated pace of environmental change outpaces honeybees' natural adaptation mechanisms. Should this trend persist, it could lead to the disappearance of several subspecies that are not genetically equipped to cope with such rapid and intense changes (Table 1). This, in turn, would have a cascading impact on pollination ecosystems and, consequently, agriculture on a broader scale.

Table 1. Critical and lethal high temperatures for five *Apis mellifera* subspecies (Abou-Shaara *et al.*, 2017; Li *et al.*, 2019).

Subspecies	Critical intolerance (°C)	Lethal temperature (°C)
<i>A. mellifera mellifera</i>	54	60
<i>A. mellifera dorsata</i>	38	45
<i>A. mellifera carnica</i>	61	66
<i>A. mellifera jemenitica</i>	66	68
<i>A. mellifera cerana</i>	57	60

There are several studies in the literature reporting accessories and designs for apiaries held in adverse climates. The insulating capacity of Langstroth hives is rather poor when compared to those in wild-dwelling colonies (Mitchel, 2015). In areas where extreme conditions exist, hive structure has resulted in thicker walls and smaller entries to reduce colony stress caused by temperature and humidity fluctuations (Mitchel, 2019). Hence, it is critical to develop hive designs that effectively reduce thermal stress while remaining inexpensive. Based on the foregoing, the goal of this review was to gather the most relevant literature on the efficiency of hive thermoregulating mechanisms in

order to identify available alternatives capable of reducing hive thermal stress caused by extreme temperatures.

CONTEXT

To compensate for environmental changes, honeybees have evolved a variety of thermoregulating mechanisms. Endothermic heat production and evaporative cooling by wing fanning are among these mechanisms for either heating or cooling the brood chamber (Heinrich, 1980; Jarimi *et al.*, 2020). However, these are not sufficiently effective under extreme conditions, either when exceeding 38 °C or below -6 °C. These strategies require excessive energy inputs during high deviations or prolonged exposures, resulting in a significant decline in worker bees. This, in turn, decreases the overall hive strength and productivity (Li *et al.*, 2019).

Former reports have demonstrated increased thermoregulation efficiency in modified hives designed for both hot and cold climates (Abou-Shaara *et al.*, 2013; Erdoğan, 2019; Floris *et al.*, 2020; Alburaki and Corona, 2021), increasing yield and decreasing mortality rates. Although conventional Langstroth hives have prevailed since 1852, exploring the use of different materials according to the local climate may offer advantages to keeping the hive microclimate within an appropriate physiologic range (Mitchell, 2015). In turn, it may help decrease colony losses and improve productivity in extreme weather. Precision Beekeeping (Zacepins *et al.*, 2015) offers accessories and communication devices to maintain hive internal conditions near optimal through cooling and heating. However, they are usually expensive for beekeepers, regardless of their operation scale (Cousin *et al.*, 2019). Besides, their handling requires specific know-how and continuous maintenance.

While most beekeeping hangs on traditional practices, the scenario has changed dramatically due to the presence of novel diseases, pests, exposure to new pesticides, and global warming. Because of these factors, the stress caused by synergistic issues and the strong oscillating weather, whether cold or hot, is becoming more dangerous (St. Clair *et al.*, 2022). Consequently, the need for developing new hives, as well as new breeds selected for specific climates, is becoming critical.

Microclimate in *Apis mellifera* hives

Temperature and humidity

As poikilothermic organisms, insects lack the capacity to regulate their internal temperature, and their metabolic functions are influenced by abiotic factors. The temperature range within brood chambers is even more narrowly defined, with minimal fluctuations between 34.5 ± 1.5 °C. Given that the developmental stages of larvae and pupae are stenothermal, their immediate surroundings must be maintained within this precise range (Stabentheiner *et al.*, 2010). Humidity is another crucial factor, as it is necessary to ensure successful egg hatching. Optimal humidity conditions are 75 % for egg hatching and 90 to 95 % for larvae survival (Ellis *et al.*, 2008).

Hive functioning rests on labor assignments such as brood feeding, food collection, wax, propolis, and honey production, hive building and cleaning, and hive defense, among others. Each worker bee is assigned to a particular task according to its temporal polyethism, which is influenced by its life stage (Tautz *et al.*, 2003). Temperature regulation is achieved through a series of mechanisms according to brood demands. Under cold temperatures (below 6 °C), heat production by bees does not reach efficient levels, causing death within exposure for less than one hour. When temperature remains between 9 and 12 °C, they may survive for several hours if appropriate thermoregulation is achieved, which, in turn, will depend on workers abundance and available resources, among other factors (Jarimi *et al.*, 2020). Honeybees are more resilient in high-temperature conditions, and their heat tolerance has been reported to be close to 54 °C.

The adaptation to high or low temperatures is also subspecies-dependent, as different genotypes can adapt to different climates (Abou-Shaara *et al.*, 2017) (Table 1). Subspecies tolerance capacity is explained by the presence of heat shock proteins, whose role is to reduce oxidative stress; differences in heat tolerance are also attributed to body size and setae abundance (Li *et al.*, 2019). As a result, it is critical to select the appropriate subspecies based on the local climate.

Social thermoregulation

Honeybee colonies in the wild are often sedentary, making them vulnerable to seasonal changes. They have responded to such challenges by establishing collective mechanisms to deal with thermal stress. The strategies used to regulate hive temperature can be passive or active.

Passive thermoregulation is based upon the proper location of brood chambers within the hive, as well as hive orientation, architecture, and building material (Jones and Oldroyd, 2006). To minimize microclimatic fluctuations, hive inner walls are isolated with propolis in a circular fashion to reduce any heat input or output and avoid undesirable air flow (Jarimi *et al.*, 2020). Propolis is made by collecting sap and resins from plants. It works as a water-proofing varnish to seal the hive. Also, it serves as a barrier to avoid the entrance of invaders, besides offering a sanitary effect, given the antimicrobial nature of resins. Therefore, passive mechanisms work by buffering the temperature differential between the hive interior and its immediate surroundings, facilitating active temperature regulation. This is an important consideration when designing hives.

Temperature fluctuations are also influenced by changes in bee density as they stay in and out of the hive. In places where temperatures drop below 15 °C, honeybees are forced to thermoregulate and warm the hive (Stabentheiner *et al.*, 2003). Thermoregulation consists of clustering together compact bee agglomerates in layers oriented towards the hive interior to reduce the air volume close to the brood chamber (Figure 1). Bees in the external layer connect their legs to create a barrier, blocking heat dissipation towards the exterior. Consequently, this conglomerate formation reduces

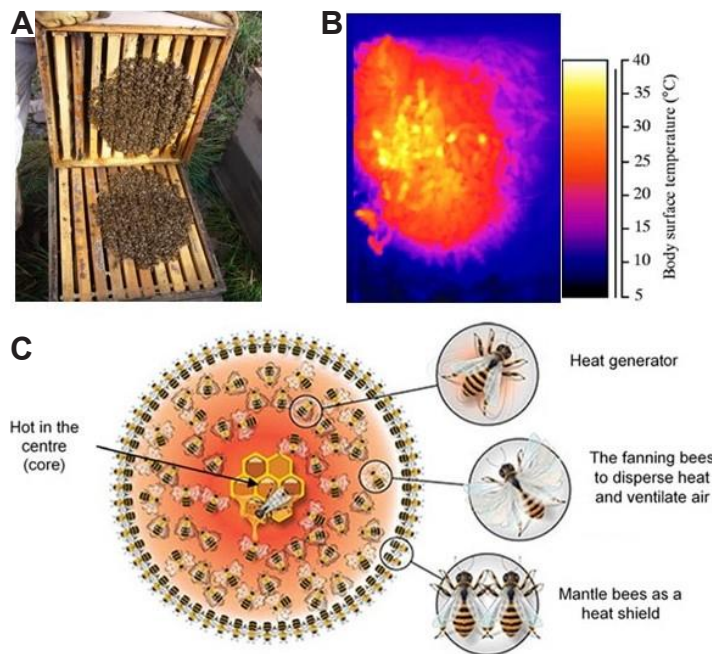


Figure 1. Hive thermoregulation system. A: bee winter conglomerates to generate and maintain heat; B: representative figure of endothermic heat and the winter bee cluster providing heat for the brood chamber; C: conglomerate infrared thermogram, temperature gradient showing how temperature decreases towards the outer layers of bees; sidebar shows the temperature corresponding to each color. Adapted from Stabentheiner *et al.* (2003).

bee body surface, which in turn minimizes heat loss by convection (Stabentheiner *et al.*, 2003; Jones and Oldroyd, 2006; Stabentheiner *et al.*, 2010).

As far as hive low-temperature exposure is concerned, bee survival is strongly compromised in the hive (Table 2). The thermal isolating mechanism becomes efficient through the release of endothermic heat by individuals within the conglomerate nuclei

Table 2. Effect of temperature and exposure on survival of Italian honeybee (*Apis mellifera L.*) colonies (Southwick and Heldmaier, 1987).

Temperature	Effect
9–12 °C	Bees may survive for several hours if their temperature matches that of the surrounding environment.
Between -2 and -6 °C	Bees die in less than one hour.
External temperature <i>ca.</i> -25 °C	A hive with 17 500 bees survived for more than 300 hours.
External temperature <i>ca.</i> -28 °C	A hive was capable to maintain an internal temperature of 31 °C for a short time.

(Stabentheiner *et al.*, 2003). Bees generate heat by unintentional quick movements contracting and releasing their chests (shaking chills), which is energetically expensive (Abou-Shaara *et al.*, 2013). When temperatures fall below this threshold, colonies face population decline due to mortality from excessive individual energy consumption. In hot weather, brood chambers are exposed to overheating; therefore, bees use evaporative mechanisms to keep temperatures down. When temperatures reach peak maximum daily values, most foragers are working outside the hive, collecting food. At night, should excess heat accumulate, most bees will remain outside the hive. This behavior helps reduce internal temperature, as long as conditions are not extreme (Zeaiter and Myerscough, 2020). However, if above threshold, bees rely on wing fanning by placing themselves in the correct formation to favor input of outside fresh air and expelling of internal CO₂-enriched hot air through the hive entrance (Peters *et al.*, 2019). This underlies the importance of keeping entrances free of obstructions to improve air circulation (Figure 2A). Evaporative cooling is another means to regulate hive internal conditions. To achieve results, bees collect and bring water to the hive to be used for lowering temperatures by wing fanning (Figure 2B).

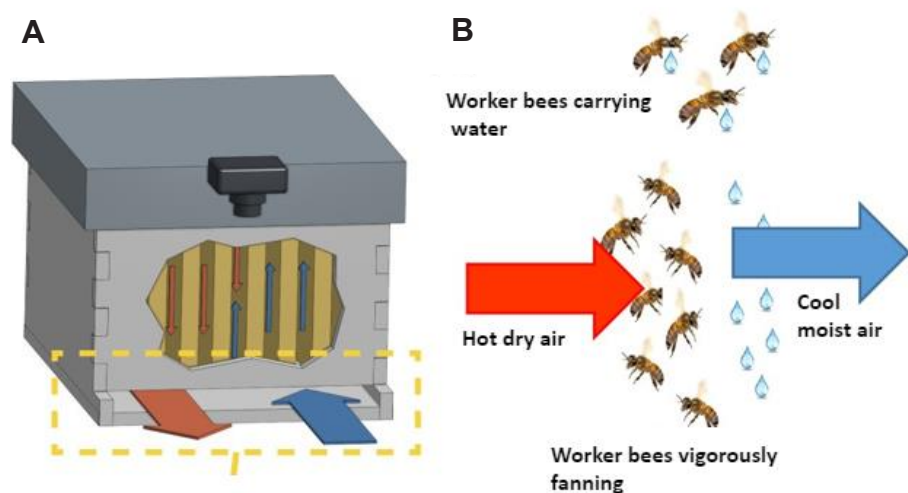


Figure 2. Hive temperature regulation in hot weather. A: Hot air expelled from the hive is replaced or exchanged by external fresh air passively entering the hive; B: evaporative cooling created by bees. Adapted from Peters *et al.* (2019) and Jarimi *et al.* (2020).

Adverse microclimate conditions

Alterations in physiology, morphology, and behavior.

A. mellifera bees developed adaptations to diverse climatic conditions through thermoregulating mechanisms as well as quick responses to microclimatic changes

within the hive. However, keeping such conditions near optimum is not always achieved. Under suboptimal conditions below 31 and above 37 °C, diverse negative effects may occur, like morphological malformations in the abdomen and legs and size changes in the proboscis, tergum, and wings (Wang *et al.*, 2016).

Groh *et al.* (2004) reported that temperature during brood influences larvae brain development; even small changes during the pupae stage dictate alterations in the development of the nervous system synaptic maturation, causing neuronal deficiencies. Concomitantly, memory and orientation are compromised, affecting exploration and foraging since their capacity to associate smells with food is fundamental, warranting success in nectar search as well as finding the way back to the hive. The same authors found that bees bred at 35 to 36 °C developed less efficient memory and orientation than those bred at 33 °C. Besides, prolonged exposure to such temperatures causes deficiencies in the waggle dance, whose function is to communicate about potential nectar and pollen source locations. A misperformed waggle dance prevents worker bees from locating food sources, given deficient communication (Tautz *et al.*, 2003).

The queen is the only female in the hive with reproductive capacity. Once reaching maturity, she goes through a mating period with drones. Mating may occur once or twice in her lifetime, keeping their sperm in a specialized organ, the spermatheca, for up to five years. Temperatures below 15 and above 38 °C cause significant reductions in sperm viability (Preston *et al.*, 2019; McAfee *et al.*, 2020). Semen viability and abundance directly affect the reproductive capacity of laying-egg queens, thus reducing hive productivity. High temperatures cause stress in queens, which in turn reduces the quantity and quality of eggs destined to become workers (Stürup *et al.*, 2013).

Thermal stress caused by cold decreases egg hatching and delays worker development; therefore, queen wellbeing impacts hive health and resilience (Preston *et al.*, 2019; McAfee *et al.*, 2020). Evidently, temperature is one factor affecting diverse physiological aspects and behavior, affecting hive productivity. However, these are just some examples of repercussions caused by thermal stress.

Global warming impact on beekeeping

Beekeeping relies heavily on stable climatic conditions for the proper development and productivity of apiaries. It has a direct impact on an essential benefit beyond honey production, as pollination is a crucial service in food production. Indirectly, it influences the socio-economic impacts of this activity. The economic value of *A. mellifera* becomes much more significant when considering crop pollination, since approximately 75 % of consumed crops depend on biotic pollination (Sosenski and Domínguez, 2018). The latest estimate calculates the global economic value of this service to be around 217 billion USD per year (Gallai *et al.*, 2008).

Global warming simulation models predict effects on food distribution, interaction, and scarcity, as well as increases in diseases and diminishing populations of pollinators, including honeybees (Menzel and Feldmeyer, 2021). Because of global warming,

beekeepers have adopted new practices, increasing investment and management expenses, resulting in reduced profits and leading to bankruptcy. Furthermore, the presence of Africanized bees in North America must be considered since they are more susceptible to changing environmental conditions, responding with migration when that occurs. Surveys in Mexico show that from 30 to 100 % of European honeybee colonies have some degree of hybridization (Alaniz-Gutiérrez *et al.*, 2016), forcing beekeepers to replace queens on a yearly basis. Most of them (56 %) point towards global warming as the main cause of colony losses in later years (Medina-Flores *et al.*, 2018).

Climate change and irregular vegetation development negatively impact beekeeping socioeconomics, forcing changes in apiary management that increase costs and affect rentability. Although studies on pesticides linked to colony collapse disorder have been under study for a long time, they focus on other threats like global warming and its relation to biological invasions and the spreading of diseases (Decourtye *et al.*, 2019).

Stress-combined factors act synergistically, causing severe damage in apiaries (Goulson *et al.*, 2015). Temperature fluctuations affect bee chemical detoxication and excretion (Kena *et al.*, 2023). Hence, temperature modulates pesticide impact in diverse contexts, depending upon exposure dosages. Previous studies have determined that exposure to neonicotinoids under cold conditions affects orientation and foraging (Monchanin *et al.*, 2019). Tosi *et al.* (2016) found that exposure to extreme temperatures (below 4 and above 33 °C) and tiametoxam affect thermoregulation capacity just one hour after exposure in Africanized bees. Medrzycki *et al.* (2010) found increased susceptibility to pesticide poisoning when the brood chamber fell 2 °C from optimum, such as in the case of dimethoate. When an appropriate thermoregulation is not achieved, many other functions are affected, such as foraging, waggle dancing, food discharge, work assignment, and flight efficiency, which decrease hive productivity and eventually lead to the loss of colonies. While many studies focus on the effect of global warming on honeybees, this review found that little attention has been directed to alternatives to help them thrive in this new situation.

A solution to increase hive thermoregulating efficiency

Hive design is of paramount importance since it serves as the home for bees. They adopt it and adapt it according to their own necessities, but to maximize thermoregulation, hive design must consider the local climate. Langstroth hives are extensively used in commercial beekeeping because of their accessible cost (Mitchel, 2019), even though their isolating capacities do not favor thermoregulation under extreme weather (Cook *et al.*, 2021). Synergic factors influence thermal stress in bees. Climatic oscillation, hard winters, and hot summer spells are creating dangerous conditions; therefore, there is a need to develop alternative, specific designs according to the local climate as well as the bee subspecies used. Because of the above, it is important to acknowledge the need for direct efforts to contribute with novel strategies to improve beehives efficiency in their thermoregulation.

Hive designs for cold climate conditions.

During winter or in regions characterized by predominantly low temperatures, colony losses are frequently observed. This situation is often aggravated by the limited availability or poor quality of floral resources, including low-quality nectar. Unlike some other species, honeybees do not hibernate. In regions with short vegetation growth seasons, bees must work diligently to accumulate sufficient food for winter preparation (Stabentheiner *et al.*, 2003; Steinhauer *et al.*, 2021). In winter, resources are used for the reproduction cycle, primarily to feed the queen and worker bees, while drones are not fed and consequently perish. This halt in hive productivity during winter makes this season the largest risk to hive sustainability (Döke *et al.*, 2015).

Winter mortality is among the main causes of beehive losses in the world. The Bee Informed Partnership monitors hive losses in the USA every year to identify causes and establish management strategies. During the 2020–2021 winter season, 32.2 % of losses were estimated. It represented an important increase as compared to the 22.6 % reported the previous winter, becoming the highest loss in the last 14 years (Steinhauer *et al.*, 2021). In Mexico, there are no official records of winter mortality; however, independent studies have reported losses of 16.4 % in the temperate sub-humid zone (Brodschneider *et al.*, 2018). Nonetheless, since climate effects may vary according to a particular region, such figures are not representative of the whole country.

Recent technologies have been implemented to face the detrimental effects of extreme temperatures, such as thermoregulating hives and intelligent hives, or so-called Precision Beekeeping (Zacepins *et al.*, 2015). These systems are based on remote monitoring to achieve the most efficient use of the available resources and improve hive productivity. They consist of a series of sensors constantly collecting data that shows the hive's condition, allowing beekeepers to access information through a mobile device. Such developments have improved beekeeping significantly since direct control over hive microclimate can be achieved by monitoring different variables all together, such as hygiene, bee population, temperature, and humidity, among many others. Despite being a very efficient management tool, their prohibitive cost, requiring costly maintenance and care, affects rentability, which may prevent their widespread adoption (IEEE, 2019).

Another economically viable alternative is designing components to improve Langstroth hives thermoregulating capacity, regardless of weather. It may be low-cost, requiring simple changes in structure and materials, bringing the best possible results (Mitchell, 2019). During the winter, it is important to insulate hives with protective materials to avoid heat loss. Since there is scarce information regarding thermoregulation efficiency in modified hives, this review shows some examples from previous studies.

It has been demonstrated that hives insulated with polyurethane improve winter insulation by maintaining temperature and humidity within small oscillations. The brood chamber temperature was 10.2 ± 0.04 °C, while in non-isolated controls it was only 9.7 ± 0.05 °C. Although this temperature range is still far from an ideal 35–36 °C, it

represents an important forward advance for not-so-extreme conditions. This study was done at mean temperatures around 0 °C. Under such conditions, achieving efficient thermoregulation is costly; however, using extra insulation helps bees improve temperature and humidity conditions and leads to less energy wear. Brood chamber humidity with and without polyurethane insulation remained at 52.2 and 62.5 %, respectively (Alburaki and Corona, 2021).

Such a response may result from wood differential absorption capacity since humidity increases during the daytime. Decreasing humidity has beneficial effects because, in winter, internal humidity rises in wooden hives, which creates an optimum condition for disease dispersal. Working in a temperate climate, St. Clair *et al.* (2022) evaluated the effects of insulating Langstroth hive upper lids with polypropylene plates. Warmer temperatures were achieved in insulated hives; even though no significant differences were found in the hive average temperatures, food consumption diminished significantly, resulting in a higher winter survival rate.

Cork was used by Floris *et al.* (2020) to evaluate its insulation capacity. It has been documented that cork has a higher insulation index than wood, and their data corroborated that. Significant improvements in hive temperature were found, averaging 34.7 °C in cork-insulated hives against 31.5 °C in controls. Since the ambient temperature was 25 °C, no significant stress was caused; however, cork-insulated hives remained at optimum temperatures for longer periods.

Although these studies showed promising alternatives when hives are modified for cold climates, the bee subspecies was not considered, and that is an important factor in temperature regulation. Materials like polystyrene and cork have low thermal conductivity as compared to conventional wood hives. Modifying hives suggests that a combination of materials may offer a synergistic effect (Wolfslehner *et al.*, 2019; Floris *et al.*, 2020).

Hive designs for hot climate conditions

Until recently, the threat posed by hot temperatures has been of little concern for beekeeping (Decourtye *et al.*, 2019). Consequently, fewer reports are available on hive design and materials to fight internal temperature increases, even though negative reports are increasing year after year (Steinhauer *et al.*, 2021). Thermoregulating mechanisms under hot temperatures bring along yield declines because of the excessive energetic wear required to cool down the hive. Besides, in arid regions, hot conditions go hand in hand with very low relative humidity. Scarce designs have been documented specifically for hot regions, although closer attention should be paid due to heat waves and global warming effects in beekeeping (Marshall *et al.*, 2020; Menzel and Feldmeyer, 2021).

Abou-Shaara *et al.* (2013) evaluated distinct types of hives for *A. mellifera carnica* and *A. mellifera jemenitica*, two subspecies native to Yemen in the Arabic peninsula, under temperatures around 37±1.2 °C. Hives showed significant results as far as collecting activity, disease presence, and average temperature, all depending on bee subspecies.

Considering both genotypes, the most efficient design was the thermoregulated hive, which was equipped with cooling and ventilation features to create a 9.8 °C reduction in internal hive temperatures. This was the most efficient model, since mellifera bees did not need to thermoregulate. However, this technology demands a high energy input, increasing production costs in an activity with marginal profits.

Erdoğan (2019) evaluated the design proposed by Abou-Shaara *et al.* (2013), although excluding the water box. The summer season reached an average of 31.2±4 °C. Neither insulating wall thickness nor bee subspecies were specified, but this was the hive with the best performance as compared with polyurethane and wood. Besides better insulation, lower temperature oscillation was recorded, and a 27.9 % increment in yield was obtained, well above the 19.8 % found in the other treatments. Another model included an external box filled with water covering the back side of the hive, which reduced the hive temperature by 8.3 °C. This design consisted of a wooden hive surrounded by insulation material and the box described above. Such a box provides not only insulation but a water source as well, therefore offering a double advantage, not only thermoregulating but also minimizing the critical search for water, crucial in deserts. Nonetheless, it's worth mentioning that humid conditions may cause sanitary issues (Eouzan *et al.*, 2019).

Although previous experiences have shown promising alternatives regarding modifications to hive components, there is plenty of room for other improvements, which must include specific climatic conditions and bee genotype since they are closely related to adaptation (Abou-Shaara *et al.*, 2017). Precision Beekeeping represents a promising and sophisticated alternative, although expensive; therefore, research and development on simple, affordable, and profitable designs are required to improve conditions for beekeepers thriving in hot, dry climates. Considering the rural nature of this economic activity, viable options are necessary (Magaña-Magaña *et al.*, 2016). Simple actions such as using above-ground structures and not placing the hives directly on the ground decrease heat gain, as well as choosing shady places for the apiary. Criteria like that rely mostly on care and interest, which have little impact on costs.

Component design perspectives for extreme condition beekeeping

It is evident that research on hive design and components is required, particularly when facing the present threats and their synergistic effects with the extreme conditions brought by global warming (Abou-Shaara *et al.*, 2013; Alatta and Alghamdi, 2015; Erdoğan, 2019; Floris *et al.*, 2020; Alburaki and Corona, 2021). Beekeeping is a sustainable livestock activity, and given the multiple benefits bees offer to ecosystems, its preservation requires important modifications to traditional management (Mitchell, 2019). Critical issues such as hive design and adaptations linked to local climate and bee genetics are to be included, should appropriate thermoregulation be considered. The joint use of wood and polystyrene as insulation is a combination of materials leading to improvements in thermal properties, reducing heat transfer and kinetic

oscillations in the hive (Erdoğan, 2019). Wood's porous nature and thermal properties are well documented, but it is also hygroscopic, implying that it retains or exudes moisture depending on environmental conditions (Mitchell, 2015). On the other hand, expandible polyurethane features low thermal conductivity, low humidity absorption, and notable buffering properties, which become important when sharp environmental changes occur. A synergistic effect of these materials can be expected, resulting in improved hive thermoregulation efficiency when extreme weather is present (Erdoğan, 2019; Wolfslehner *et al.*, 2019). Its low cost is another factor to consider.

CONCLUSIONS

This comprehensive literature review highlights the crucial importance of thermoregulation in honeybee (*Apis mellifera* L.) colonies, particularly in the context of climate change and extreme temperatures. Bees have developed ingenious mechanisms to cope with adverse environmental conditions, but it is essential to consider additional measures to enhance hive productivity while minimizing thermal stress, given its physiological and behavioral consequences. This review contributes to improving our understanding of how bees confront thermal challenges and underscores the need for concrete measures, such as hive modifications, to safeguard these valuable pollinators in an ever-changing world and promote their resilience in the face of climate change and other stressors.

The modification of hives to reduce thermal stress includes the use of insulating materials and ventilation systems to maintain a more constant temperature inside the hive, protect bees from extreme temperature fluctuations, and facilitate their thermoregulatory efforts. Due to the increased thermal buffering, bees do not waste energy attempting to regulate temperature, redirecting this energy toward food collection, which results in increased egg laying, worker population, and hive productivity. Furthermore, these modifications must be tailored to local conditions, since what works in one environment may not be effective in another.

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