Top of page: *Five bees facing the inside of the hive ventilate on the flight board. (Peters, J.M., O. Peleg, and L. Mahadevan. 2019. Collective ventilation in honey bee nests. J. R. Soc. Interface. 16:20180561). Courtesy of L. Mahadevan.*

Thermoregulation in Honey Bees
Part 1

by Frédéric Eggers de Villepin

Introduction

Thermoregulation is one of the processes within the broader framework of homeostasis, which enables an organism to maintain its physiological parameters within a range conducive to optimal functioning.

Briefly, on the scale of a honey bee colony, the homeostasis of the nest is conditioned not only by temperature, but also by humidity levels, and by the balance of oxygen and CO2 levels, in relation to the conditions of its environment. Thanks to the specialized receptors on its antennae,[1] the bee is perfectly able to measure these parameters, and can also trigger individual and collective action programs to keep them under control. Simply put, thermoregulation is the process by which the balance between the production and loss of thermal energy is controlled in honey bees.

Let's continue with a few definitions: The adult bee is a poikilothermic and endothermic insect, i.e., its body temperature is not constant and varies over a wide tolerance range — etymologically, it is irregular — and it has the capacity to heat its own body and, if necessary, its immediate environment. When bees do not actively produce heat, they are said to be ectothermic, dependent on a heat source external to their body.

When these dispositions are combined with behavioral capacities that operate on a colony-wide scale or only at group level, we speak of social thermoregulation. As with many other activities in a honey bee colony, the aim here is to collectively solve a problem. For example, in the presence of brood, in both cold and hot periods, honey bee colonies maintain brood temperature within a "tropical" temperature range of between 34.5°C and 36°C (94.1 and 96.8 F).

The high adaptive value of this social thermoregulatory capacity is one of the driving forces behind the bee's gradual expansion from its primitive tropical niche to temperate regions. What's more, the evolutionary history of bee social life has made the bee the only insect from cold regions to maintain a warm climate within its habitat (Seeley, 2019), and to do so with astonishing precision.

The study of these behaviors and physiological mechanisms goes back a long way.

According to Bernd Heinrich (2007), the first intuition concerning the warming of an insect's body correlated with its activity dates back to the first half of the 19th century. At the beginning of the 20th century, insect body temperatures were measured (Himmer, 1925), and the great stability of honey bee nest temperatures despite changing external conditions was noted (Hess, 1926).

In 1926, a study of social thermal equilibrium in the winter colony was published (Himmer, 1926). Two years later, Heinz Dotterweich made a connection between increased thoracic temperature and flight preparation in a sphinx butterfly, but the first attempt to uncover the underlying physiological processes seems to date from 1941 (Krogh and Zeuthen, 1941).

From the second half of the 20th century to the present day, a massive body of knowledge on the behavioral and physiological mechanisms of thermoregulation in bees and their combinations has been produced.

In this article, we focus on thermoregulation in honey bees, particularly at the colony or group level.

The importance of temperature for adults and brood

The adult bee tolerates a wide range of ambient and body temperatures, but a thorax temperature below 18°C (64.4 F) will impair its ability to activate its flight muscles and compromise its respiratory function. Below 7°C (44.6 F), the bee falls into a kind of coma and then dies (Stabentheiner et al., 2003) (Goller and Esch, 1990). Exposed to temperatures of 45°C (113 F) or above, the bee dies within a few hours (Seeley, 2019).

What about the brood? Harmonious and optimal development of the brood — i.e., in the shortest possible development time — requires that the nest temperature be constantly maintained in the 34-36°C (93.2-96.8 F) range. Although the brood produces some heat through its own metabolism,[2] it cannot compensate for any deviations from the optimum range by itself.

Eggs and larvae are less sensitive to momentary deviations outside this range.[3] Pupal development, on the other hand, is far more demanding.

In fact, studies show that the performance of adult bees will be all the poorer if they develop at a temperature even one degree below or above the range indicated above. Even very slight cooling at the pupal stage significantly slows development. Prolonged exposure to a temperature of 32°C (89.6 F) is likely to result in malformations in nymphs (Stabentheiner et al., 2010) and impaired performance (e.g., lower frequency and quality of dances) and learning in adults (Tautz et al., 2003; Groh et al., 2004; Jones et al., 2005). Exceeding the ideal range from above also leads to deleterious disruptions (Medina et al., 2018; McAfee et al., 2020).

T.D. Seeley (2019) reports further examples of the benefits of thermoregulation from work carried out in the 1930s. Since then, it has been known that cooling to 30°C (86 F) for just a few hours leads to the development of ascospherosis (plastered brood disease), but that this infection is halted when the temperature is raised and maintained at 35°C (95 F) (Maurizio, 1934). More recent studies have also demonstrated a rise in brood temperature in response to infection (Starks et al., 2000).

Homeostasis control in the nest

As we've seen, a rise or fall in temperature inside the nest, even by just a few degrees, poses a direct threat to individual and collective survival, in both cases introducing damaging disruptions to brood development and compromising the colony's growth rate and efficiency.

The bee's great sensitivity to temperature variations, and its ability to regulate its own, goes hand in hand with the evolutionary history of bee social life. Depending on the need, a graduated response is provided at colony level, either behavioral — cluster formation, ventilation, water collection and dispersal — and/or physiological — thermogenesis. These mechanisms can be combined.

Whether it's a question of regulating an upward or downward drift in one of the parameters on which nest homeostasis depends, the response is a self-organized cooperation of individuals within the colony.

A. Stabentheiner and colleagues (2021) point out that the thresholds at which different countermeasures are engaged in the face of temperature variation vary considerably.[4] He attributes this to the fact that the self-organization of thermoregulation relies on a multitude of bees scattered throughout the nest, each individual constituting a "sensory and regulatory unit," reacting to different thresholds of temperature and hygrometry[5]; these same conditions differing from one point to another and also varying over time (the temperature between combs is not constant and variations in heat flows are perceived in a staggered manner). A film[6] associated with the above study illustrates these spatio-temporal fluctuations in air temperature between the central frames of a 10-frame hive.

Let's now look at how the bee can generate heat, and how this individual capacity benefits the colony as a whole.

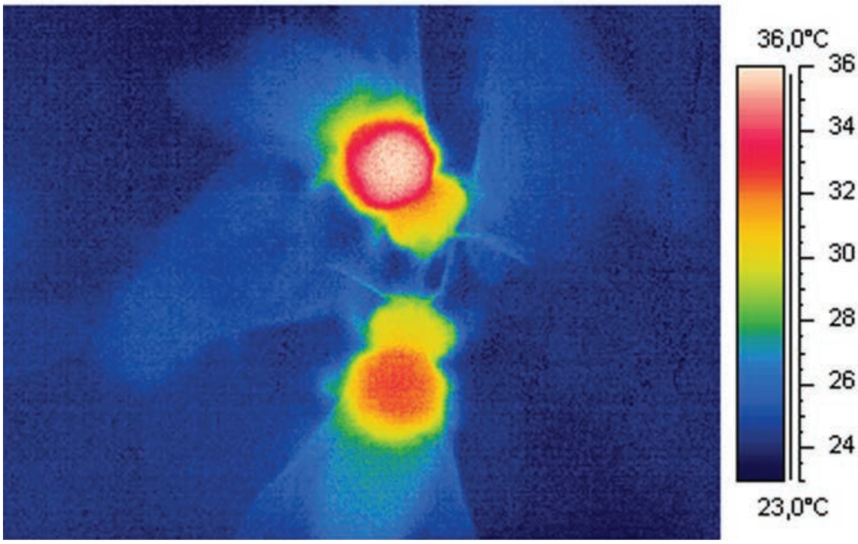

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Fig. 1 Thermogram of bees in endothermic and ectothermic states. (Stabentheiner, A., H. Kovac, and R. Brodschneider. 2010. Honey bee Colony Thermoregulation — Regulatory Mechanisms and Contribution of Individuals in Dependence on Age, Location and Thermal Stress. PLOS ONE. 5:e8967).

Endogenous thermoregulation to benefit the colony

According to T.D. Seeley, the bee's ability to maintain a warm climate inside its cabin is derived from its evolutionary adaptation to flight. The bee has a powerful flight musculature, composed of dorsal and longitudinal antagonistic wing muscles. The author tells us that: "In flight, the weight/power ratio is 500 watts/kg, compared with the maximum power developed by an Olympic rower, which is 20 watts/kg. Consequently, to fly, the bee consumes a great deal of energy, but generates a lot of heat." In fact, 80% of the energy produced is converted into heat, but paradoxically, this heat is first required to produce the muscular movement of flight that generates this heat: The bee cannot take flight unless its muscle temperature is first raised to 27°C (80.6 F).

But how does the bee cope? Seeley adds: "Over the course of evolution, bees have developed the ability to preheat their muscles. To do this, the antagonistic elevator and depressor muscles are activated simultaneously — isometric contraction generating heat without producing wing vibration." The same tetanic contraction mechanism is used to warm the brood combs. It is accompanied by high fuel consumption and intensified respiration.

So, here is found the way to produce heat on demand, over and above that produced by the body's basic metabolic functions!

However, when conditions call for it, not all bees contribute to heat production. A distinction must be made between bees that will actively generate heat through this mechanism — endothermic bees — and the more numerous bees that will not — ectothermic bees — i.e., resting adults and very young bees that, before their 7th hour of life (Stabentheiner et al., 2003), are not able to generate heat with their flight muscles.

Figure 1 shows, in the foreground, two bees in an endothermic state with a high thoracic temperature. On the left and right, the silhouettes of two bees in the ectothermic state can be seen; they produce no heat other than that of their basal metabolism, and their temperature is close to that of the environment.

Without the aid of a thermographic camera, it's not easy to distinguish between endothermic and ectothermic workers. However, we can

Courtesy of Jürgen Tautz

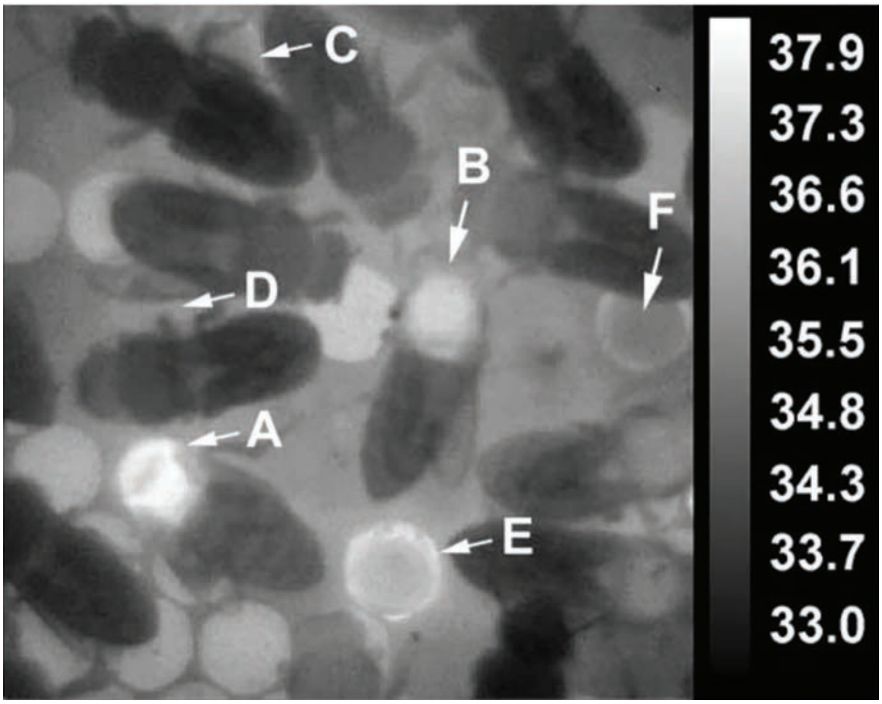

Fig. 2 *Thermogram of worker bees on capped brood. (Kleinhenz, M., B. Bujok, S. Fuchs, and J. Tautz. 2003. Hot bees in empty brood nest cells: heating from within. J. Exp. Biol. 206:4217–4231).*
Capped cells are shown in gray, while open cells can be recognized by their hexagonal outline. Bee [A], with a thoracic temperature of 37.9°C (100.2 F), is about to enter a cell adjacent to three capped cells. Bee [B] has just left the empty cell in the center of the image, which is at 37.3°C (99.1 F). Bees [C] and [D] do not produce heat (cold thorax). Heat production during cell visits is indicated approximately when the cell interior and thorax (visible as a ring-like structure around the dark silhouette of the cold abdomen) begin to "glow" with increasing intensity [E] and [F].

sometimes observe a worker with her thorax resting against an alveolus, remaining in this posture long enough to generate enough heat to raise her thoracic temperature to 40°C (104 F) and warm the alveolus by a few degrees. At other times, a bee will enter an alveolus adjacent to brood and warm it up, remaining there for up to 30 minutes.

Courtesy of Thomas D. Seeley

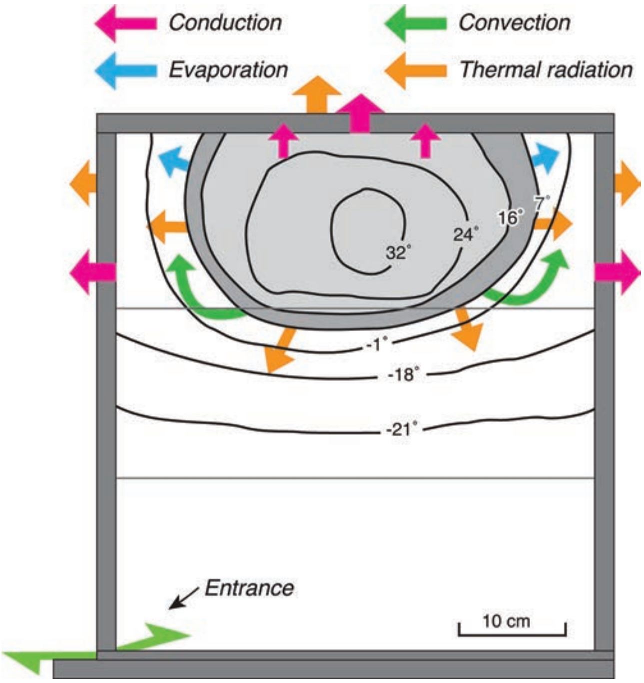

Fig. 3
Isothermal curves of a cluster of bees. (Seeley, 2019) The Lives of Bees: The Untold Story of the Honey bee in the Wild.

The Figure 2 thermogram illustrates these behaviors.

Endothermic bees are generally smaller in number, which, given the high energy cost of endothermy, helps preserve honey resources. However, as you'd expect, the lower the temperature, the greater the number of bees involved in heat production. They are mainly found on the brood, but outside this zone, if the temperature outside the brood is not constant and as long as the cluster has not formed, any effort to produce heat contributes to reducing the temperature gradient between the brood and its immediate surroundings, and a little beyond. This limits heat loss from the brood. This behavior also helps ectothermic bees maintain their body temperature above 20°C (68 F).

The workers who are deliberately endothermic are not the only ones to generate heat. Drones and even foragers help maintain nest temperature. Males stand on or around the brood and also use their flight muscles to generate heat (Harrison, 1987; Kovac et al., 2009). Which goes to show that they don't just eat and hope to be mated, as is often claimed (and maybe that's not all). Back at the nest, foragers display a warm thorax.

COMBATING HEAT LOSS

As already mentioned, thermoregulation is all about balance. And, of course, there are major differences between habitats: In terms of thermal efficiency, the simple wooden crates of our modern beehives are certainly no match for a natural cavity of appropriate volume in the hollow of a thick-walled tree.

T.D. Seeley (2019) details the various causes of heat loss (Figure 3): "Heat is lost by conduction through the ceiling and combs, by convection with air currents passing through the porous cluster and the rest of the cavity, by evaporation due to adult respiration and evaporation from the surfaces of the wet bodies of larvae and wet combs. Finally, by the thermal radiation that the colony emits in the direction of all surrounding objects (rays, walls)."

The colony has a number of means at its disposal to reduce thermal energy loss, including the choice of the cavity to be used (size and conformation, location, exposure),[7] the reduction of the flight hole (propolis), and the formation, conformation and location of the cluster.

More in the next issue.

Footnotes

1 Among all receptors, thermoreceptors are located at the tips of the antennae and have a sensitivity of half a degree (Lacher, 1964)1964.

2 The temperature of capped brood in the absence of workers is 26°C to 27°C (78.8-80.6 F). (Kronenberg and Heller, 1982).

3 Larvae have a higher metabolic rate than pupae (Kronenberg and Heller, 1982).

4 This variability had already been observed, and was put to good use to improve temperature stability over a wide range (Peters et al., 2019).

5 Genetic diversity within the colony is at the root of these differences (Jones et al., 2005).

6 **https://link.springer.com/article/10.1007/s00359-021-01464-8#additional-information**

7 **T.D. Seeley** hypothesizes that the bee would evaluate the thickness of the walls of a future passenger compartment (impact on thermal conductivity).

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ABJ thanks L'Abeille de France for permission to reprint this article from its September 2023 issue.

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