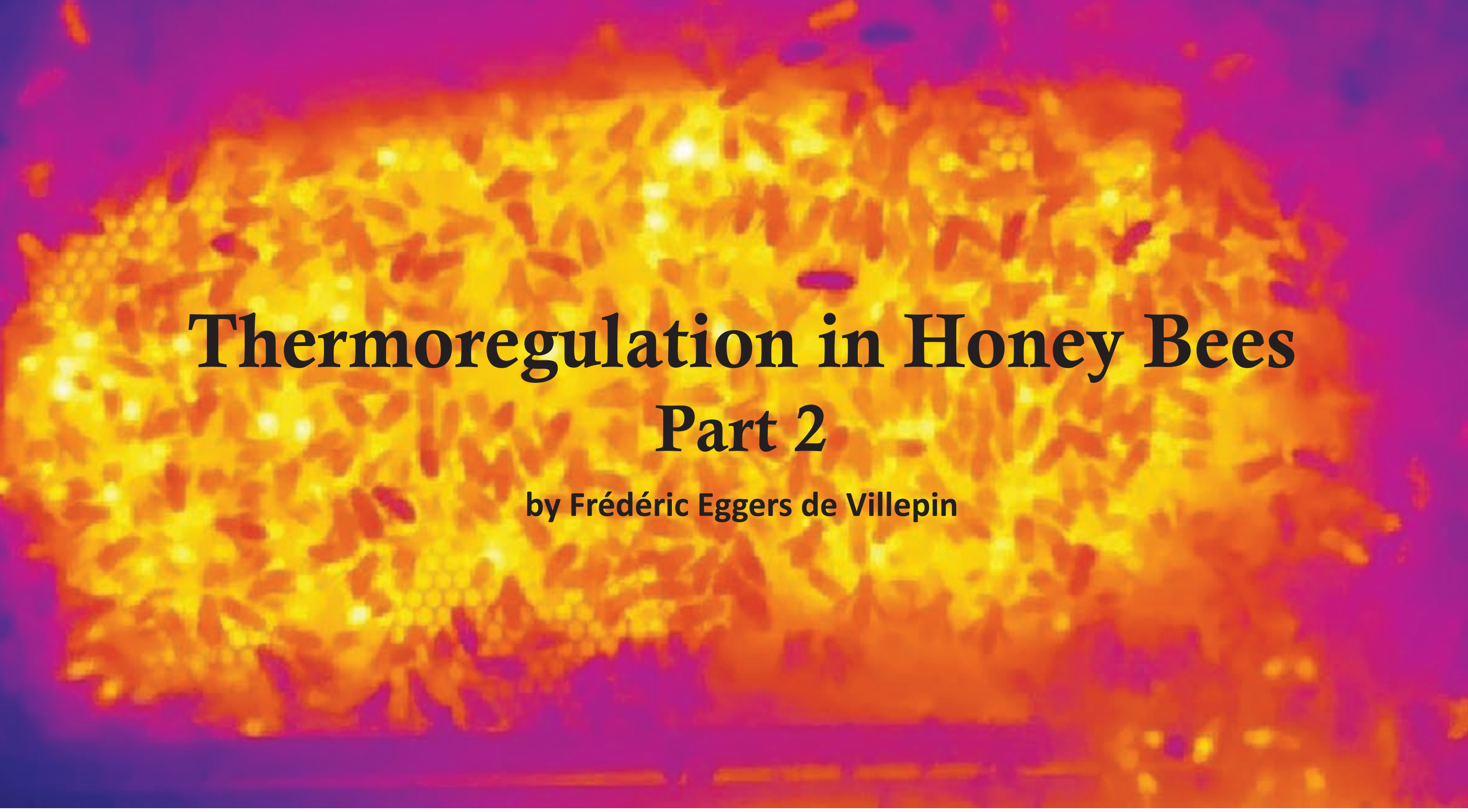

Thermoregulation in Honey Bees
Part 2

by Frédéric Eggers de Villepin

... continued from last month

Cluster formation

The need for the colony to survive the winter period mainly involves two distinct and complementary mechanisms: cluster formation and thermogenesis. The phenomenon of cluster formation should be seen as the implementation of a remarkable thermal insulation device.

T.D. Seeley (2019) explains that the surface area of a bee's body in contact with the outside air is around 3.8 cm^2, while that of a cluster made up of 15,000 bees with a diameter of 18 cm is around 1,000 cm^2. The contact surface of our bee's body is therefore reduced, on average, to around 0.067 cm^2. This greatly reduces heat loss.

Before cluster formation begins at a temperature of around 14°C (57.2 F), the density of bees on the brood increases as the temperature drops (Kronenberg and Heller, 1982; Stabentheiner et al., 2021). Conversely, when the temperature rises significantly, the density of bees on the brood decreases.

A rise in temperature is accompanied by cluster expansion, and at 14°C, the cluster gradually expands until it ruptures at a higher temperature. Conversely, the lower the temperature, the tighter the cluster. This reduces convection (less air passing between the inside of the cluster and its periphery), heat exchange surface area (between individuals and the cluster) and evaporation. The cluster reaches its contraction limit at around -10°C (14 F). The volume occupied is around five times smaller than at 14°C (Owens et al., 1971).

The first discovery of the cluster's organization is due to the work of C.D. Owens in 1951, which distinguished two parts — see Figure 3 in Part 1. The outer one, between isotherms 7 and 16, comprises several layers of bees in tightly packed rows between the combs, all with their heads turned inwards. They occupy the empty cells to form an insulating mantle, aided by the downy fleece of their thorax. The inner layer, less densely packed, allows the bees to circulate, feed and ventilate the cluster.

J. Harrison (1987) observed that "in clusters ... bees in the innermost layer were significantly younger than bees in the outermost layer. Day-old bees and drones were always located in the innermost layer of the cluster."

Thermogenesis in the cluster ...

When we talk about clusters, we almost forget that they are broken up by rays. The image below (Figure 1) would almost lead us to speak of clusters in the plural. In reality, it's the outer edges of the frames that are cold and give the illusion, but from the center of one frame to the next, there's a continuum of temperature.

As we'll see, depending on whether brood is present or not, the colony doesn't develop the same thermogenesis effort.

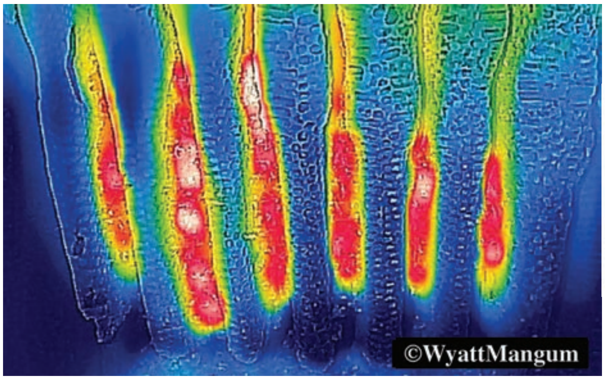

Fig. 1
Thermogram of the frames of a cold-season hive. (Dr Wyatt Mangum: "Winter is coming, see bees survive in bitter cold," American Bee Journal, 11-2018). Courtesy of the author.

Top of page: *Thermogram of a cluster of bees. (Stabentheiner, A., H. Kovac, M. Mandl, and H. Käfer. 2021. Coping with the cold and fighting the heat: thermal homeostasis of a superorganism, the honey bee colony. J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol. 207:337–351). Photo under Creative Commons BY 4.0 license.*

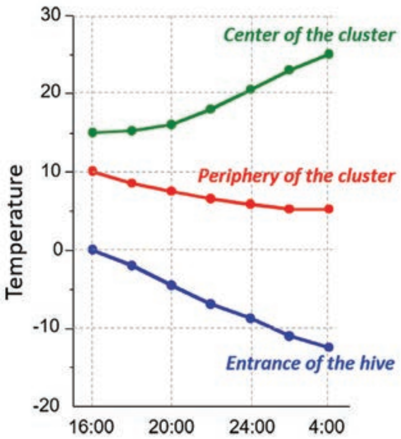

Fig. 2 *Influence of the drop in outside temperature on the cluster on a winter's evening. Schematic by Clotilde Randriamampita based on Fahrenholz et al., 1989, quoted in Kievits, 2009.*

... IN THE ABSENCE OF BROOD

According to T.D. Seeley (2019), in the absence of brood, the temperature will be maintained in such a way that the bees forming the mantle at the periphery of the cluster do not fall into a deep lethargy at the risk of leaving the cluster and freezing to death at the bottom of the cavity. The temperature in the center of the cluster will therefore not fall below 18°C (64.4 F) and will remain above the fatal threshold of 7°C (44.6 F) in its outermost layer.

Figure 2 illustrates the evolution of cluster temperatures — core and periphery — as a function of the drop in outside temperature.

In a study by A. Stabentheiner and colleagues (2003), thoracic temperatures of 12°C (53.6 F) were recorded in outer layer bees, and 9°C (48.2 F) in the abdomen (remember that bees face the center of the cluster). At these temperatures, the bees' metabolism slows down and consumes few resources.[1] At the same time, the thorax temperature of bees in the center of the cluster rose to 30.4°C (86.7 F).

These are our endothermic bees which, although they are the least exposed individually, do their best to generate heat from the center of the cluster, and not from its periphery where the thermal energy would be immediately lost. They represent around 15% of the bees present on the central frames. The Figure 3 thermogram illustrates this configuration.

The study also reveals a little-known behavior: Endothermic bees periodically pass through the cluster, visiting its outermost layer, only to re-enter a few seconds later. It is assumed that it is these bees that play a role in regulating cluster temperature, as it seems that it is the temperature of the mantle and not the temperature of the cluster center that guides the heat production effort (Stabentheiner et al., 2021), since this is where the bees closest to the lethal level are located.

... IN THE PRESENCE OF BROOD

As already mentioned, in the presence of brood, the temperature will be maintained in the range 34-36°C (93.2-96.8 F) with a daily variation of 0.5°C, whether the outside temperature drops below 0°C (32 F) or rises above 40°C (104 F) (Seeley, 2019).

This time, unlike in the case of a broodless colony, it is the temperature requirement of the capped brood that guides the regulation effort. According to a 1982 study (Kronenberg and Heller), the most stable temperature is found at the level of the capped brood, on which, moreover, the form-

Courtesy of Anton Stabentheiner

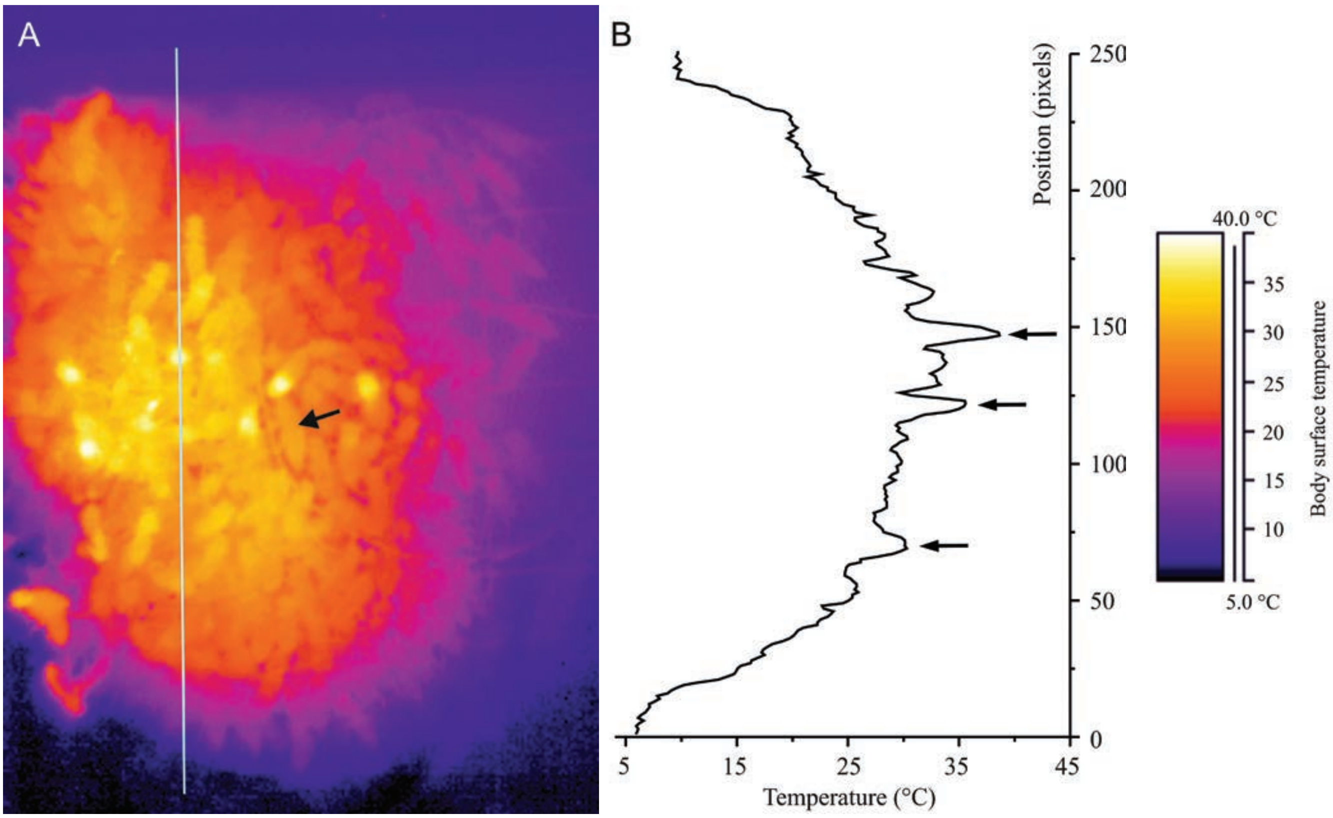

Fig. 3 *Thermogram of a winter cluster of bees on the central frame (excluding brood). (Stabentheiner, A., H. Pressl, T. Papst, N. Hrassnigg, and K. Crailsheim. 2003. Endothermic heat production in honey bee winter clusters. J. Exp. Biol. 206:353–358.)*
(A) Note the warm thoraxes of endothermic bees (yellow and white spots) and the queen (black arrow). Visiting bees from the cluster surface are visible in the lower left. (B) Temperature profile along the line shown in figure A; the black arrows correspond to the thoraxes of endothermic bees on the line. The temperature was 5.5°C (41.9 F) near the cluster and 3.7°C (38.7 F) outside.

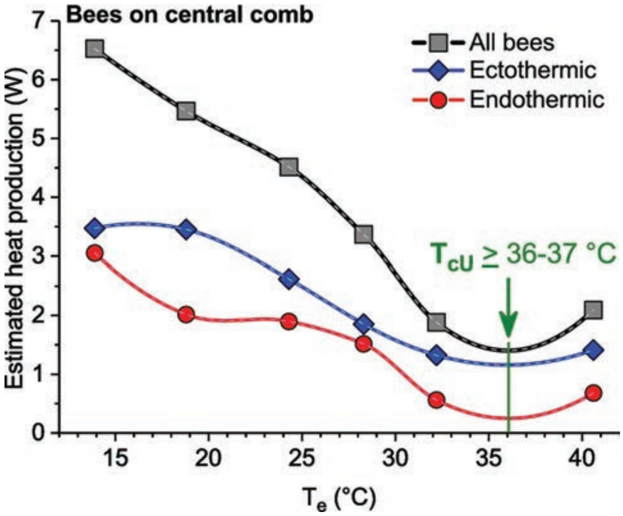

Fig. 4 *Estimation of cumulative heat production by bees on the central comb as a function of ambient temperature (Te). (Stabentheiner, A., H. Kovac, M. Mandl, and H. Käfer. 2021. Coping with the cold and fighting the heat: thermal homeostasis of a superorganism, the honey bee colony. J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol. 207:337–351). Photo under Creative Commons BY 4.0 license.*

ing cluster is centered. The same study indicates that brood of the same age is generally found mirrored on either side of a frame, and that the surface area common to both sides is of the order of 80%, forming an insulating layer. The authors also hypothesize that the bees measure the temperature not at the surface of the frame, but below it, and that the brood itself can inform the workers of the need for thermoregulation. Another study (Stabentheiner et al., 2021) argues that worker behavior is elicited by chemical and tactile stimuli emitted by the brood, as previously suggested by the claim that capped cells produce stimulatory pheromones that are more attractive to workers than those in open brood (Koeniger, 1978).

As Figure 4 shows, while the metabolic temperature of ectothermic bees is lower than that of endothermic bees, the former, which are far more numerous, collectively produce more heat, but this is not enough.

Nest cooling

As mentioned above, a rise in temperature beyond the tolerance range is a major risk for the colony. Above 40°C (104 F), it can also lead to the collapse of wax combs.

A rise in temperature triggers appropriate response behaviors at different thresholds: reduction in the density of bees on the brood, ventilation, and collection and dispersal of water within the nest. These responses involve the mobilization of workers and a reallocation of tasks within the colony (Johnson, 2002), in line with the intensity of the risk.

Bees are able to lower the temperature on and around the brood below their own body temperature. By maintaining a lower temperature between the frames, a flow is created that is able to evacuate heat away from the brood area (Stabentheiner et al., 2021). This flow will be directed out of the cockpit by the ventilation effort of the workers on the flight board.

From the scientific literature, J. Kievits (2019) tells us that in the absence of active ventilation (which every beekeeper has observed) and, therefore, at moderate temperatures, "natural" flows not actively produced by the bees circulate inside the cabin. This natural convection can be linked to the masses present (bees, gaseous accumulation such as CO2 or water vapor) as well as to spatial variations in temperature.

At an environmental temperature of 34-36°C (93.2-96.8 F), the density of bees on the brood is at its lowest, and is limited to the number of bees needed to care for and cool the brood (Stabentheiner et al., 2021). If necessary, some of them leave the nest.

Air ...

If ventilation is always present, if only to renew the air, but also to evacuate excess humidity (nectar concentration), it intensifies when the indoor temperature reaches 24-25°C (75.2-77 F) (Stabentheiner et al., 2021).

In a study published in 2019, J. Peters and colleagues attempt to understand how a self-organized ventilation strategy is set up from the cabin entrance to induce incoming and outgoing air flows, and how bee groups form, break up, move and reconfigure as temperature varies. The study also discusses the use of airflow-mediated communication to support the self-organization process, as well as the influence of genetic diversity on the success of the strategy.

A video[2] associated with the above-mentioned article illustrates temperature fluctuations on the flight board, clearly highlighting incoming and outgoing flows.

Figure 5 shows fanners in action on the flight board. Other ventilators may be at work inside the hive, in a coordinated fashion.

... and water

At around 31°C (87.8 F) outside, the next countermeasure is to add water, which is spat out in droplets inside and outside the cells (Lindauer, 1954; Stabentheiner et al., 2021).[3] The surface area covered by droplets can be up to 6% of the surface area of the hive's central frames.[4] As we have seen, cooling the air between the combs encourages heat to escape from the combs.

When it comes to supplying the hive with water, supply is determined by demand. This is expressed in the transfer time between a collector bee and an inner worker (Kühnholz and Seeley, 1997). If worker bees are less eager or show a frank lack of interest in a collector bee, the supply of water decreases or dries up.

In addition to ventilation, bees also use tongue snapping (Lindauer, 1954) to accelerate water evaporation. This is described by the author as follows: "The evaporation of water is further

F. Eggers de Villepin

Fig. 5 *Fanners on the flight board. You can recognize a fanner by its characteristic position — back arched, wings squared, motionless and firmly planted on its legs. Here, the fanners are grouped together on the left-hand side of the flight deck, in the same orientation.*

intensified by other bees which expel droplets from their mouths by constantly clicking their proboscis and extract them film-like with it. Proof is provided that this "proboscis flapping" is not only used to regulate temperature, but also to thicken nectar."

In order to stabilize the internal climate of the cabin, intensified ventilation and droplet dispersion begin even before the bees' active or passive heat production is reduced to a minimum (Stabentheiner et al., 2021).

The energy cost of cooling is said to be higher than that of winter heating.

Lessons for beekeepers

In this article, in the light of scientific knowledge, we have taken a look at the complex phenomenon of thermoregulation in a honey bee colony.

At the level of our beekeeping practices, this knowledge sheds light on our understanding and should encourage the most novice among us to think more carefully about aspects such as overwintering, humidity management and hive insulation, as well as non-intrusive hive monitoring.

We won't go into detail here on these aspects, as they would require a whole article of their own!

Acknowledgments

I'd like to thank the scientists who inspired me, in particular Thomas D. Seeley for his kindness and his admirable book "The Lives of Bees: The Untold Story of the Honey Bee in the Wild" (Princeton University Press, 2019) and Anton Stabentheiner.

Footnotes

1 **K.V. Nerum (Van Nerum and Buelens, 1997).** shows that low oxygen levels in the winter cluster cause relative hypoxia, which in turn lowers the metabolic rate. The economic and longevity benefits are significant.

2 **https://royalsocietypublishing.org/doi/suppl/10.1098/rsif.2018.0561#secSuppl** (See supplemental material number 2.)

3 This study reports a difference of up to 4.6°C between the temperature measured at a droplet site and that of adjacent cells, with an average difference of around 2°C.

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

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Recommendations for beginner beekeepers

- Wintering strong colonies ... in thermally adapted and prepared living quarters (insulation for the cold season is not the same as insulation for the warm season);
- Sufficient quantity and quality of winter reserves, including and especially around central frames;
- Presence of a quality water point, equipped to prevent drowning;
- Limited disruption of colonial homeostasis by the beekeeper. Reasoned and limited frequency of visits, coupled with non-intrusive monitoring;
- Preservation of the propolis mortar that seals the frame cover, as bees cannot restore it in the cold season;
- Hive insulation: size, thickness, materials used (thermal, hygrometric and radiative properties) and moisture management (mainly in the cold season);
- Location, exposure to humidity, wind and sun, orientation of the hive.