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How do bees breed?

Thermal Conduction in Bee Hives

ECMI Modeling Week

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Abstract

Thermal regulation in honeycombs is essential for the breeding process of bees. This regulation is achieved by the bees by contracting their flight muscles at a high rate in order to generate heat. In practice, heat is diffused by the bees either by juxtaposing itself to the pupae, or by heating adjacent cells. First, a review of previous attempts on modelling thermal heat diffusion inside a honeycomb is examined, before looking into the numerics of such a system. In the numerical part, the honeycomb heat problem is discretized via the finite element method. Heating and cooling of the honeycomb by cell-heating bees is simulated. The simulation is used to observe the isolation properties of different substances.

1 Introduction

Outside of human societies, the honey bee colony is considered to be one of the premiere examples of cooperative group functioning—an example of optimal social behaviour that has evolved entirely through the process of natural selection [5]. Along these lines, the honey bees have learned that by maintaining the temperature and humidity of the hive to a strict range (roughly $33 - 36^{\circ}C$) this not only allows for the preservation and storage of the hive’s food and honey, but also optimises the development and health of the offspring and workers. It is this natural ability of the bees to properly distribute the heat in their homes that will be of concern to us; more specifically, in this paper we wish to model and explain the transfer of heat that occurs in a typical bee hive.

Let us first discuss the structure of a typical bee hive. The structure of most honey bee hives (or honey bee combs) consist of a mostly flat vertical panel (the honeycomb), with two half-combs separated by a midrib surface (Figure 1). These half-combs are covered by hexagonal cells of wax, which are either empty, or filled with honey, pollen, or the offspring (pupae). Furthermore, the hive is typically structured in layers, with the brood kept at the bottom center, and with the honey to the sides and above the offspring. Of course, the health and



Figure 1: A typical honey bee hive.

development of the offspring is paramount; in order to maintain the pupae-filled cells at the optimal temperature of 33 to $36^{\circ}C$, the worker bees have developed two interesting strategies, both of which use the bee’s unique ability to heat its thorax to an astonishing $38.1 - 42.4^{\circ}C$ by contracting its flight muscles, when properly decoupled from the flight mechanism. The first strategy is to place this

warmed thorax onto the cap of a pupae-filled cell; by doing so, it is able to raise the temperature of the cell by up to 3.2°C . The second strategy is for the bee to enter an adjacent vacant cell, and then to heat the cell for a longer period of time (~ 30 minutes), while cyclically generating heat. Here, the heat of the cell can range from 32.7 to 40.6° for times ranging from a few minutes to tens of minutes [1].

2 Mathematical Formulation

There has been some work done in the field of heat transport in a honeycomb, especially by biologists. Broad surveys have been done concerning the lives of the hive as a whole and particular bees inside it. We know quite much about certain aspects of bee swarm and even about heat distribution. But unfortunately this information is mostly descriptive. There are not many papers on the mathematical side of this phenomenon and numerical modelling. We have found one paper by J.A.C. Humphrey and E.S. Dykes [1] concerning mathematical modelling of this particular problem. We have been inspired by their work and used similar model in our numerical simulations.

2.1 Model description

In this section, we will review the assumptions made in [1] for the construction of the model.

First, we begin with a (half)comb represented by a 20×20 grid of hexagons. Each hexagon has a depth of $L_d = 14.4\text{mm}$, a side length of $L_w = 2.3\text{mm}$, and a cell wall thickness of about $70\mu\text{m}$. These cells contain honey, pollen, pupae, a cell-heating bee, or are left empty (and thus filled with air). Table [] lists the key thermal and physical properties of each cell, identical to those numbers used by [1]. The current model is then completed by adding an identical half-comb, separated a normal distance of $L_s = 14\text{mm}$ away. In the following, we will review five assumptions, fully elucidated in the aforementioned article.

- **Dominance of cell-heating bees vs. cap-heating bees**

The thermal effects of the cap-heating bees can be ignored in comparison with the cell-heating bees. Essentially, this is because the snug fit between bee and cell guarantees much more conduction and radiation, scaled to the surface area of all six cell walls, compared to the conduction and radiation via the smaller surface area of the cap.

- **Wax walls contribute to negligible resistance**

The extreme thinness of the walls ($\sim 70\mu\text{m}$) contributes to a negligible amount of normal heat transfer—several orders of magnitude lower than the heat transfer due to conductance.

- **Radiation effects are ignored**

- *Bee to wall:* Because the bee-to-wall spacing is so small ($\sim 0.1\text{mm}$) the radiative heat transfer be ignored in favour of pure conduction.
- *Between two halfcomb surfaces:* We can make the assumption that in a healthy bee-hive, the two facing comb surfaces (about the midrib) are of essentially the same temperature and thus the radiation exchange will be minimal.
- *Within cells:* The heat transfer between opposing cell walls in an air-filled cell is subdominant to the conductive transfer, essentially due to the fact that the maximum temperature deviation between the two walls is relatively small (from a numerical estimation)

- **Convection is ignored**

Within the comb cells, the smallness of the characteristic length-scale implies that the Rayleigh number is sufficiently small that convection can be ignored. Moreover the situation in the gaps between halfcomb surfaces is similar, with the separation length insufficient to produce any significant transfer via convection.

The above recapitulation of the work by Humphrey and Davis [1] thus implies that the dominant mode of heat transfer throughout a beehive can be captured using the two-dimensional heat equation in each cell, with continuity and flux conditions at the cell walls.

2.2 Equations and solution

The cells in the honeycomb are represented by a continuum of materials with different physical properties. Authors assume that every cell is completely filled with appropriate material. They use the unsteady heat equation in calculating quantitative. This equation governs the heat transport in every cell and is given by

$$\rho c_p \frac{\partial T}{\partial t} = k \left(\frac{\partial^2 T}{\partial x^2} + \frac{\partial^2 T}{\partial y^2} \right) + G. \quad (1)$$

where ρ is the density, c_p - specific heat, k - thermal conductivity and T is the temperature at (x,y,t) . The function G represents a source of heat. It could be either pupae or cell-heating bee.

At the interfaces of adjoining cells (here 1 and 2) the boundary conditions have to be imposed.

$$T_1 = T_2 \quad (2)$$

$$k_1 \frac{\partial T_1}{\partial n} = k_2 \frac{\partial T_2}{\partial n} \quad (3)$$

where $\frac{\partial T_2}{\partial n}$ denotes the normal derivative to the interface.

Above equations give the heat distribution in every cell. Authors separated the solution procedure into three cases taking $T_i = 34^\circ C$ as an initial condition in i th cell.

- *Case1* : Calculation of the steady-state temperature assuming that there are no cell-heating bees. All heat is generated only by the pupae.
- *Case2* : Using previously obtained steady-state temperature profile as an initial condition. The calculation is performed with one heating-bee present. Bee heats the cell for 10min and then either vacates the cell or remains in it and generate heat in a slower rate.
- *Case3* : The same process as in *Case2* but with 5 cell-heating bees.

All the numerical computations in the paper were carried in FEMLAB, a finite element method software operating in MATLAB environment. Furthermore, we will focus on the third case in this report.

3 Numerical Implementation

3.1 Problem Description

The numerical implementation of the problem requires modelling the heat equation on a subdivided domain. On each subdomain, heat equation is fulfilled with different coefficients. Between the subdomains, on the interfaces, continuity is prescribed.

The problem is formulated in the following way. Let a bounded domain $\Omega \subset \mathbb{R}^2$ be split into N subdomains, Ω_i with

$$\bigcup_{i=1}^N \bar{\Omega}_i = \Omega.$$

Each subdomain Ω_i should be of equal size with hexagonal shape representing a honeycomb cell. Ω should hence model a cut-out of a honeycomb. For illustration of Ω , see Figure 2.

The boundary conditions are of static Dirichlet type:

$$T(\cdot, t) = g_0(\cdot) \text{ on } \partial\Omega \tag{4}$$

for all times $t \in (t_0, t_1)$. The initial conditions are:

$$T(\cdot, t_0) = T_0(\cdot) \text{ on } \bar{\Omega}. \tag{5}$$

3.2 Input Data

There are a total of five different substances that can fill a honeycomb cell – honey, pollen, pupae, air gaps, as well as the cell-heating bees occupying some of the gaps. Hence, there are five different types of parameters for the heat

	ρ ($kg\ m^{-3}$)	c_p ($J\ kg^{-1}\ K^{-1}$)	k ($W\ m^{-1}\ K^{-1}$)	G ($W\ m^{-3}$)
honey	1400	2300	0.60	0
pollen	420	2720	0.15	0
pupae	996	4180	0.61	10^3
air	1.1774	1005.7	0.02624	0
bee	996	4180	0.61	2.9×10^5

Table 1: Physical properties of different substances occupying a honeycomb cell.

equation coefficients on each Ω_i . The specific values of the parameters are listed in Table 1.

The length of one side of the hexagonal cell Ω_i is 2.3 mm. The boundary condition is prescribed to 34 °Celsius ($g_0 = 307.15$ Kelvin).

3.3 Problem Setup

Two programs, `MATLAB`'s PDE Toolbox and `COMSOL` were considered for simulating the problem numerically. Due to its restrictive capabilities, `MATLAB` was rejected in favor of the more powerful and user friendly `COMSOL`.

The domain Ω is represented by $N = 400$ cells arranged in a rectangular 20 by 20 grid.

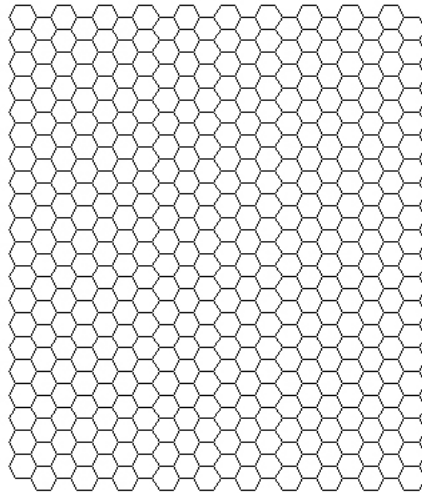


Figure 2: Domain Ω , a 20 by 20 grid of cells Ω_i .

Figure 2 shows the domain Ω drawn in `COMSOL`. The subdivision of Ω into the cells Ω_i is represented by the distinct hexagonal shapes in the figure. Each cell is filled with a different substance – honey, pollen, pupae, air gaps and cell-heating bees. The positioning of these five substances within the model is an

attempt to replicate their arrangement in a real-life honeycomb. Figure 3 shows this specific arrangement.

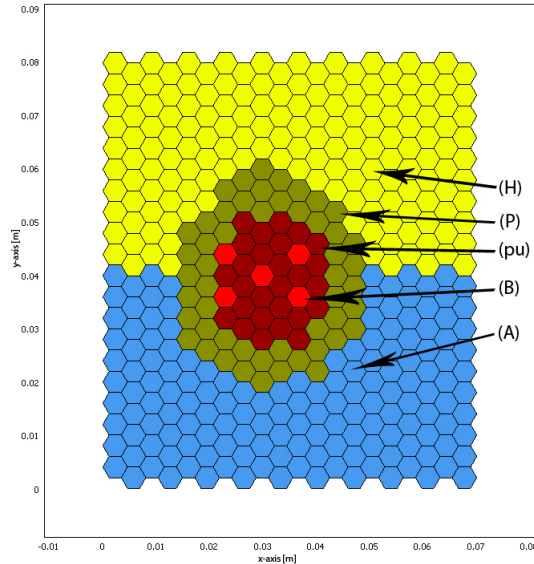


Figure 3: Arrangement of different substances within the honeycomb model. From top to bottom: (H) honey, (P) pollen, (pu) pupae, (B) cells with heating bees, (A) air.

For the sake of notation, let $B \subset \{1, \dots, N\}$ be introduced as a set of subdomain indices marked with (B) in Figure 3.

3.4 Simulation

In the simulation, the honeycomb is at first heated up, then cooled down. According to literature, cell heating bees heat the honeycomb for around ten minutes, after which they vacate their cells (thus a cool down takes place). In the simulation, the temperature in the honeycomb will be observed at 10 minute intervals, up to a total of 20 minutes. The time intervals are marked accordingly (in seconds):

$$\begin{aligned} t_0 &= 0 \\ t_1 &= 600 \\ t_2 &= 1200. \end{aligned}$$

The interval $[t_0, t_1]$ will be called the heating stage, whereas the interval $[t_1, t_2]$ will be called the cooling stage.

In the first ten minutes, heating will be simulated. The heat equation coefficients in cells Ω_i with $i \in B$ (bee-occupied cells) will be set to “bee” from Table

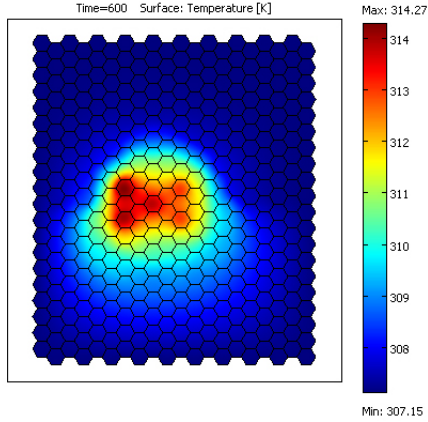


Figure 4: Temperature T in the honeycomb at the end of the heating stage, at time t_1 . The temperature scale ranges from 34 to 41.92 °Celsius.

1. The initial value of the heating problem will be 34 °Celsius on the whole domain Ω . In Kelvin:

$$T(\cdot, t_0) = 307.15 \text{ on } \bar{\Omega}.$$

Then in the next ten minutes, cooling effect will be observed. The bees vacate their cells, so the equation coefficients in cells with bees are then changed to the coefficients corresponding to air-filled cells. No effort is made to model the bees behaviour post-vacating the cell. The initial value of the cooling problem will be the solution obtained at time t_1 of the heating problem:

$$T(\cdot, t_1) \text{ on } \bar{\Omega}.$$

3.4.1 Results

The temperature spread after the heating stage is displayed in Figure 4, whereas the temperature after the cooling stage is displayed in Figure 5.

In Figure 4, one immediately notices the location of the five cell-heating bees by the highest total heat accumulated at their cells. The overall heat is concentrated around the cell-heating bees.

One also notices a certain asymmetric distribution of heat. The vertical asymmetry, appearing in a pear-shaped form, is caused by the different heat-specific properties of air, which is on bottom of the honeycomb, against honey, which is on top (see Figure 3). The slight horizontal asymmetry comes due to the original non-symmetric setup of the substances in the honeycomb (also see Figure 3).

In Figure 5, after cooling took place, the maximum heat has decreased and the overall heat has spread throughout the honeycomb.

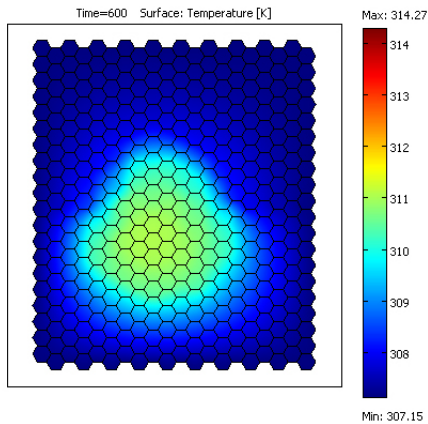


Figure 5: Temperature T in the honeycomb at the end of the cooling stage, at time t_2 .

The simulation procedure gives the opportunity to numerically evaluate different arrangements within the honeycomb. The possibilities vary from rearranging the substances within the honeycomb to organizing a periodic heating cycles for bees.

Were one to formulate an optimization problem for the honeycomb, one could use this simulation technique to find the optimal numerical solution. However, even the formulation of such problem can be a rather complex task, as it is at first unclear what functional and under what constraints must be optimized.

3.4.2 (Basic) Efficiency Test – Isolation of the Pupae Cluster

A very simple efficiency test can be conducted. In Figure 3 one can observe that bees surround the pupae cluster with a perimeter of pollen. However, they could equally well surround it with honey or just leave those perimeter cells empty, surrounding the cluster with air. The question is: why would bees use pollen as the surrounding substance around the pupae cluster instead of another substance?

Using the simulation model, one can change the perimeter material from pollen to honey or air to observe the heat diffusion in the honeycomb. As one is interested in keeping the pupae warm, the pupae temperature with respect to time will be observed. A surface integral of the temperature over the pupae cells will be used as the efficiency function.

A surrounding material a will be called more efficient than material b , if the surface temperature of the pupae cells is higher by a than by b at all times t . Alternatively put, if the pupae cells will heat up faster during the heating stage and cool down slower during the cooling stage by using surrounding material a instead of b , then a is more efficient than b .

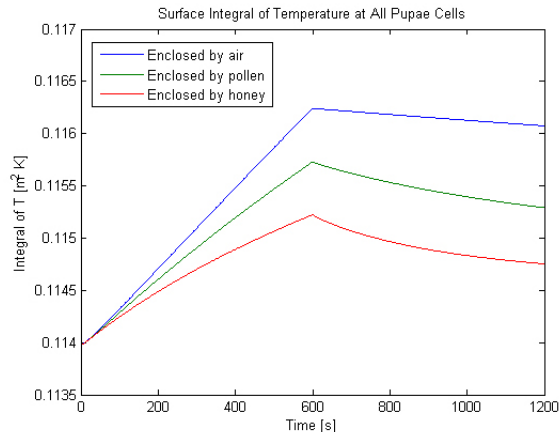


Figure 6: Surface integral of temperature function T_i over all pupae cells with respect to time. The kink in the plots appears at the 10-minute point where the problem changes from heating to cooling.

Figure 6 displays the graphs of surface integrals of temperature in pupae cells for three different enclosing substances: air, pollen and honey, over a 20-minute interval. It can be observed that air ranks as the most efficient of the three, pollen comes on second place, whereas honey is the least efficient thermic-enclosure for pupae. The possible explanation for why air is not used by bees is due to its storage inefficiency – the empty space should be occupied by some substance. Between the two materials, which can be stored around the pupae, bees prefer pollen, as it gives better isolation than honey.

Naturally, the isolation effect of the three substances that is observed in this test is the direct consequence of their thermic properties. Nevertheless, this test gives an on-hand example of how a very basic optimization problem is attempted to be solved numerically by simulation.

4 Analytical Considerations

In this section, we will say a few words about the potential for analytical approaches to the honeycomb problem. We will keep the analysis brief for one simple reason: As was shown in the previous section, the numerical solution of the honeycomb problem is a simple exercise for a standard finite-elements package, and while analytical approximations can indeed be developed, their solution will likely be contingent on the evaluation of analytically intractable integrals and boundary conditions—which will, in the end, still require a numerical computation. Thus, a complete and in-depth analytical study may not be warranted, given that the full time-dependent problem is so easily solved

numerically.

4.1 A back-of-the-envelope computation

Suppose we were to reduce the two-dimensional steady-state 20×20 beehive problem to a problem in only one dimension. This would consist of taking a vertical ($x = \text{const}$) or horizontal ($y = \text{const}$) slice of Figure 3. In the following, we will hold x constant and non-dimensionalize $\bar{y} = yL_H$, where $L_H = L_W \cot(\pi/6) \approx 3.8\text{mm}$ is the width of a typical height (cross-section) of a honeycomb. Equations (1)-(3) would thus reduce to

$$\frac{d^2 T(\bar{y})}{d\bar{y}^2} = -\frac{G_i}{k_i L_w^2} \quad (6)$$

$$T(0) = 307.15 \text{ K} \quad (7)$$

$$T(20) = 307.15 \text{ K} \quad (8)$$

$$T(i) = T(i+1) \quad i = 1, \dots, 19 \quad (9)$$

$$k_i \frac{dT(i)}{d\bar{y}} = k_{i+1} \frac{dT(i+1)}{d\bar{y}} \quad i = 1, \dots, 19 \quad (10)$$

Now each beehive is divided into distinct layers, each layer containing honeycombs of a single property. Clearly, by the continuity and flux conditions, solving the heat equation in each ‘hexagon’ is equivalent to solving the heat equation in the entire layer. Thus we see that the solution of the above set is a piecewise quadratic equation,

$$T(y) = \left(-\frac{G_i}{k_i L_w^2} \right) y^2 + B_i y + C_i, \quad i = 1, \dots, 19.$$

where B_i and C_i are constants to be determined by the matching conditions.

For example, we can solve for the centre-most layer which contains (in increasing y): 4 air, 2 pollen, 3 pupae, 1 bee, 2 pupae, 3 pollen, and 5 honey cells. The global solution is then displayed in Figure 7 (left).

There is obviously a gross overestimation of the maximum temperatures involved; the reason for this is the inherent asymmetries in the bee-hive. For example, the lone bee at the centre of the hive is surrounded by six (cooler) pupae-filled cells. It is then obvious that the effective heat source of the bee is overestimated in our 1D estimation (which allows only a flux in two directions). A ‘fudge-factor’ can be imposed on the source strengths:

$$G_{\text{pupae}} \mapsto \frac{G_i}{\tau_{\text{pupae}}} \quad i = 9, 10, 11, 12, 14, 15$$

$$G_{\text{bee}} \mapsto \frac{G_i}{\tau_{\text{bee}}} \quad i = 13$$

Using $\tau_{\text{bee}} = 32$ and $\tau_{\text{pupae}} = 5$, we produce Figure 7 (right).

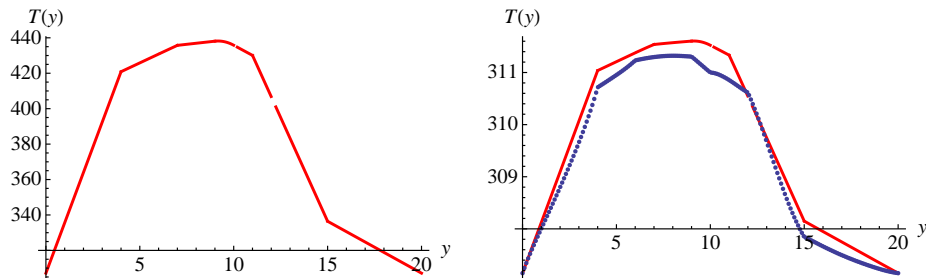


Figure 7: The 1D approximation (red curve) in the left figure overestimates the solution profile because the heat is only allowed to diffuse in one direction. We can define an ‘effective’ source term, G for the bee and pupae cells; this provides a better agreement with the full 2D numerical results (dotted, blue) shown in the right figure.

Now obviously, the above procedure is decidedly non-mathematical(!) A mathematical reduction of the true two-dimensional problem to a one-dimensional one would be impossible, for the true steady-state temperature is a *global* problem. However, the point of the above analysis is to produce a back-of-the-envelope approximation that nevertheless preserves some of the qualitative (if not quantitative) features of the full problem.

4.2 The full problem

In consideration of the previous subsection, we now see that the solution of Equations (1)-(3) is equivalent to solving the time-dependent heat equation in several distinct layers with continuity and flux matching conditions—that is, the polygonal structure of the problem can be entirely ignored, except at the very boundaries. Neglecting this fine structure, we can say that the solution would be well approximated by the solution of the heat equation in a rectangular domain (representing the honey/air boundary) with inner annuli and circular regions (representing each of the different cells).

In particular the solution in each layer can then be expressed in terms of Green’s functions. However, because of the nontrivial boundary conditions, it is unlikely that we would be able to generate a closed-form solution which would shed much light on the issue(s) involved. To put it simply: when the full numerical solution is so easily computed and studied, it is unlikely that a convoluted analytical solution would provide any more illumination than already available.

Where a more analytical approach might be fruitful is if the small-scale structure of the hive is more complex, but still ordered in some regular (often periodic) fashion. In that case, asymptotic methods like homogenization or multiple-scale could be used to reduce the problem to a simpler effective problem. Similar methods have been applied to diffusion problems on periodic lattices (see [4], [2], or [3])

5 Discussion

Some assumptions about the model should be verified by real-life experiments. For example, acknowledging that radiative and convective effects can be ignored in the heating problem should be verified, and other heating sources originating from the honey-comb's environment should be discussed. Furthermore, long-time asymptotics could be affected by convection and radiation, because the contrary have not been shown.

Deriving an analytical solution for this diffusion problem is rather complicated compared to the speed in which the system is solved numerically. A sufficient simulation layout has been defined, and enables in-depth exploration of the organisation of the bee-hive in terms of thermal heating strategy. Those strategies can be compared by simulation of different scenarios. The problem of finding the optimal heating strategy should be investigated, together with the associated optimal bee-hive structure in order to obtain a deeper understanding of the magnificent precision bees can attain when it gets to regulating the temperature inside the honeycomb.

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