



Flow currents and ventilation in Langstroth beehives due to brood thermoregulation efforts of honeybees

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ABSTRACT

Beekeepers universally agree that ensuring sufficient ventilation is vital for sustaining a thriving, healthy honeybee colony. Despite this fact, surprisingly little is known about the ventilation and flow patterns in bee hives. We take a first step towards developing a model-based approach that uses computational fluid dynamics to simulate natural ventilation flow inside a standard Langstroth beehive. A 3-D model of a Langstroth beehive with one brood chamber and one honey super was constructed and inside it the honeybee colony was distributed among different clusters each occupying the different bee-spaces between frames in the brood chamber. For the purpose of modeling, each honeybee cluster was treated as an air-saturated porous medium with constant porosity. Heat and mass transfer interactions of the honeybees with the air, the outcome of metabolism, were captured in the porous medium model as source and sink terms appearing in the governing equations of fluid dynamics. The temperature of the brood that results from the thermoregulation efforts of the colony is applied as a boundary condition for the governing equations. The governing equations for heat, mass transport and fluid flow were solved using Fluent[®], a commercially available CFD program. The results from the simulations indicate that (a) both heat and mass transfer resulting from honeybee metabolism play a vital role in determining the structure of the flow inside the beehive and mass transfer cannot be neglected, (b) at low ambient temperatures, the nonuniform temperature profile on comb surfaces that results from brood incubation enhances flow through the honeybee cluster which removes much of the carbon-dioxide produced by the cluster resulting in lower carbon-dioxide concentration next to the brood, (c) increasing ambient (outside) air temperature causes ventilation flow rate to drop resulting in weaker flow inside the beehive. Flow visualization indicates that at low ambient air temperatures the flow inside the beehive has an interesting 3-D structure with the presence of large recirculating vortices occupying the space between honey super frames above the honeybee clusters in the brood chamber and the structure and strength of the flow inside and around the honeybee clusters changes as we increase the ambient air temperature outside the beehive.

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1. Introduction

1.1. Motivation for the problem

Gas exchange is an important consideration in habitats of social insects which are self-constructed as it is needed to bring fresh oxygen supply into the habitat from the free atmosphere outside as well as to prevent accumulation of carbon-dioxide and other by products of animal metabolism inside the habitat. In addition, fluid flow inside these habitats should aid the insect's ability to

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generate and maintain their own body temperature (thermoregulation). The predominant mode of ventilation in these habitats is passive with the flow currents inside arising from the temperature and concentration gradients setup due to the activities of the insects themselves. Biologists have been always interested in exploring the structure-function relationship that exists in the design of these self-constructed habitats. For example, researchers (Scott Turner, 1994; Korb and Linsenmair, 2000a, 2000b) have identified that some species of fungus cultivating termites, Macrotermitinae, construct elaborate mounds to setup a micro-environment inside their habitat which enhances the gas exchange. In this study, we are interested in modeling the micro-environment that exists inside a beehive, which are man made structures (basic design credited to Langstroth) used by beekeepers to raise colonies of honeybees (*Apis* spp. Hymenoptera).

Honeybees (*Apis* spp. Hymenoptera) have the amazing capacity to function as independent individuals and in the colony, as a super-organism of tens of thousands coordinated individuals (Moritz and Southwick, 1992; Southwick, 1991). The honeybee colony lives and breathes as a unit (Heinrich, 1981a). Honeybee colonies are also remarkable because they incubate their brood (developing larvae and pupae) with narrow temperature limits outside of which the brood matures improperly and dies (Seeley, 1995; Crane, 1990; Heinrich, 1985). Human beings have exploited honeybee colonial productivity for millennia, and have taken cavity nesting species into their care by providing artificial homes (hives) for the honeybees (Wilson, 2007). European races of the Western Honeybee (*Apis mellifera* L.) are the mainstay of most commercial (Crane, 1990; Bonney, 1993) and hobby beekeeping in Europe, Africa, parts of Asia, Australia and the Pacific and the Americas. The scientific understanding of honeybee biology, including how the living, breathing, temperature regulated colony works has been incorporated in modern beekeeping (apiculture). A beekeeper (or apiarist) rears honeybees in order to collect honey and beeswax, for the purpose of pollinating crops, or to produce bees for sale to other beekeepers. Modern beekeeping is a popular hobby activity as well as a thriving industry (Crane, 1990).

Ventilation in a beehive removes by-products of honeybee metabolism, such as carbon-dioxide and water vapor, supplies fresh oxygen, and is necessary for the production of honey, which results from drying of nectar (Crane, 1975). Moreover, ventilation in a beehive plays a vital role in transporting and distributing the fumigants applied by the bee keepers for the purpose of pest and infection management (Kevan, 2007). Studies (Oldroyd, 2007) to understand the causes of rapid collapse of honeybee colony sizes worldwide (termed colony collapse disorder) have identified lack of proper incubation of the brood as one of the causes among others for the collapse. Understanding the flow inside the beehive and finding ways to enhance ventilation may alleviate the stress on the honeybee colonies and aid them in proper incubation of their brood. The need for good ventilation in a beehive and its role in maintaining a healthy beehive has been long recognized by practicing beekeepers (Root and Root, 2005). This is reflected in the numerous patents filed by practicing bee keepers each referring to different modifications (e.g. adding multiple openings on the front face of the beehive near the top, special top covers) to the standard Langstroth beehive design. Despite the consensus about the vital role of ventilation, little published information is available on the flow and its features inside the beehive and how behavioral and physiological aspects of honeybees affect this flow. Assessing the flow structure in an active beehive experimentally is difficult due to the tight air space inside the beehive and the presence of honeybees which interfere with instrumentation by covering them with propolis. In this study, we used a model based approach using computational fluid dynamics tools to simulate the flow inside the beehive. For the purpose of simulations, based on our own visual inspection of beehives and inputs from local beekeepers, a geometric model of a beehive and its contents was constructed, and the governing equations of fluid dynamics coupled with equations describing the metabolism of honeybees were solved numerically using a commercial CFD software.

To lay a framework for understanding the simulations done in this investigation, we present in Section 1.2 a brief overview of the biology in a beehive explaining the necessity for honeybees to actively control the thermal environment as well the different understood mechanisms by which the honey bees achieve them. In Section 1.3, we review the earlier modeling work related to heat transfer in honeybees as well as the relevant published experimental findings that we use in constructing our model.

1.2. Biology in a beehive

A functional colony of honeybees in a single beehive consists of three types (castes) of honeybees: one queen bee, around 20,000–30,000 worker bees and, at certain times of the year, around 500 drones. The queen and workers are female, the drones are male. Each caste is essential to the life of the colony and each has specific roles and duties. The queen has an average life span of 2–3 years and its primary duty is to lay eggs, normally 1000–1500 per day. The eggs are laid in the hexagonal wax cells built into the comb by the worker bees. After the eggs are laid and hatch into larvae, the workers feed this brood. Once the larvae have matured the cells are capped by the workers and the larvae pupate. They then develop further by metamorphosis to emerge from cells as adult bees. The cells and their developing young are referred to as brood. Drones have an average life span of a few weeks and their primary function is to mate with the queen. Drones do not live through the winter. The worker bees with a life span of a few weeks to months (depending on time of the year) are the primary work horses in a beehive. They feed and rear the brood, keep the brood warm, forage for food nectar and pollen, produce honey from nectar, collect water and pollen, and generally maintain the beehive.

The colony in a beehive is active year round, but their level of activity and population size varies with the seasons (Bonney, 1993). During the winter months, the population and activity level is low and the bees survive by feeding on their honey stores. In the winter, the colony does not have brood. Starting later in winter, the queen recommences laying eggs, bee activity and population size increases, and brood rearing accelerates. The social organization of honeybees means that they act collectively to maintain and support the colony.

Honeybees maintain temperature and humidity levels inside their hive within narrow limits. In particular, they maintain the brood on the combs at a steady temperature in the range 33–36 °C (Kleinhenz et al., 2003; Seeley, 1995; Southwick, 1991; Moritz and Southwick, 1992). This constant temperature is crucial for the normal growth and development of the brood (Tautz et al., 2003). Deviations from this range can occur when the ambient air temperature changes. This can be detrimental to the development of the brood. If this is the case, the worker bees engage in behavioral and physiological activities to either warm up or cool the brood.

At low ambient temperatures, whenever the brood temperature drops below the needed range of temperature, worker honeybees engage in different strategies to warm up the brood. One such strategy they employ is to heat their thoraces through muscular activity and press their warm thoraces onto capped brood cells for several minutes at a time (Bujok et al., 2002), such honeybees are referred as cap heating honeybees. The second strategy the worker honeybees employ is to warm themselves up, to enter empty comb cells among the brood, and to dissipate their body heat to the brood cells around them (Kleinhenz et al., 2003); such honeybees are referred to as cell heating honeybees. In both the case of cell and the cap heating honeybees, the bees increase their body temperature by isometrical contraction of the bee flight muscles (Seeley, 1995; Crane, 1990). In addition to these heating strategies, the honeybees also try to insulate and reduce the heat loss from the brood by crowding in the brood area (Kronenberg and Heller, 1982; Harrison, 1987). Another physiological response consists of changing the metabolic response with ambient temperature (Kronenberg and Heller, 1982).

As ambient air temperature rises above 30 °C, density of the honeybees comprising the cluster reduces (Kronenberg and Heller, 1982) and honeybees inside the beehive engage in fanning to enhance the flow inside the beehive (Chadwick, 1922; Lindauer,

1971; Simpson, 1961; Hazelhoff, 1954). In addition, during hot summer days, worker bees have been observed to orient themselves just outside the entrance to the beehive and engage in fanning hot air out of the hive body (Bruman, 1928). This fanning behavior is triggered also in response to rising concentrations of respiratory gases inside the beehive (Hazelhoff, 1954; Lacher, 1966; Seeley, 1974). In addition to fanning response, honeybees have been observed to use evaporative cooling wherein they spread the water amongst empty cells present in the brood area which then evaporates and removes heat from the brood area (Von Frisch, 1950; Lindauer, 1971).

1.3. Previous work on ventilation of a beehive

Experimental investigations in the past relating to ventilation in beehives have focussed mainly on how honeybees as a colony initiate and maintain flow inside the beehive via fanning under different conditions (Jones and Oldroyd, 2006; Southwick, 1985; Southwick and Moritz, 1987; Kronenberg and Heller, 1982). Only few experimental investigations (Hazelhoff, 1954; Wedmore, 1947) have focussed on documenting the ventilation in a beehive that occurs in the absence of active fanning. In addition, the fore mentioned studies describe the flow that arises during the ventilation only qualitatively. Therefore values of measures commonly used in quantifying ventilation in engineering enclosures are not available for a beehive. The word “ventilation” as suggested in Hazelhoff (1954) has been used in two different contexts in the honeybee literature, at times referring to the respiration of an individual honeybee (Lighton and Lovegrove, 1990), or to the flow generated by the fanning of honey bees (Southwick and Moritz, 1987). We describe it as the process that exchanges air between the beehive and ambient outside the beehive, with this process resulting in setting up air flow inside the beehive. Of these three contexts, the flow due to fanning response has garnered the most interest in the scientific literature (Kronenberg and Heller, 1982; Wedmore, 1947; Hazelhoff, 1954; Simpson, 1961; Southwick and Moritz, 1987; Fahrenholz et al., 1989). Most of those studies focussed on the understanding the external conditions that triggered the fanning response, such as high ambient temperature or high levels of carbon-dioxide. The results of those investigations lacked details on the strength of the flow setup by these fanners and how that affects the conditions inside the beehive. The ventilation induced by coordinated fanning of honeybees at the entrance to a small bodied beehive was studied by Southwick and Moritz (1987). A periodic fanning behavior of the honeybees at the inlet was observed, which consisted of periods of rest when passive influx of fresh outside air occurred followed by periods of continuous intense fanning when warm stale air inside the beehive was driven out of the beehive. Only Hazelhoff (1954) has studied the flow inside the beehive in the same context as we have in our study. Hazelhoff (1954) reported significant flow in and out of the beehive even in calm summer weather in the absence of external wind. The beehives used in their study, unlike the one modeled in our study, had two additional air inlets, one in the front of the beehive, and another one on the top cover. Hazelhoff (1954) reported that displacement mode of ventilation was active, where the air entered through the lower inlet and left through the top openings. The air leaving the beehive was analyzed to contain 0.6–0.7% carbon-dioxide. The air flow current at the exit was measured to be in average, 0.1 L/s, a much higher value than might be expected from a beehive with only one inlet. Hazelhoff (1954) also observed the fanning mechanism of the bees wherein they oriented themselves with their head facing the entrance of the beehive and fanned their wings almost like in flight but while holding a firm grip on the bottom board, setting up a draft

pushing the air outside from inside the beehive. This fanning behavior was initiated both in response to external heating of the beehive as well as introduction of carbon-dioxide from outside the beehive.

1.4. Previous modeling work related to honeybees

Earlier modeling studies related to honeybees primarily focussed on trying to understand their ability as a colony to actively thermoregulate in cold winter temperatures. More recently, Humphrey and Dykes (2008) through their numerical simulations studied the effectiveness of the different brood thermoregulation strategies (cell, surface heating) which were observed in the experiments of Kleinhenz et al. (2003) and Bujok et al. (2002). In all the earlier modeling studies, the effect of flow through the honeybee cluster was neglected, an assumption valid for tightly packed cluster present during the winter which is not the case during the late spring and summer when the clustering of honeybees inside the beehive is known to be less dense. The honeybee metabolism, involves both heat and mass transfer with the air, out of these two mechanisms, the former has been accounted for in all the earlier models while very few have accounted for the latter (Omholt, 1987a).

The mathematical models studying thermoregulation in honeybee colonies during the winter have focused on two configurations, first where the cluster of honeybees is present outside the beehive (reproductive swarms) (Basak et al., 1996; Myerscough, 1993), and the second where the honeybee cluster is present inside the beehive (Lonvik and Omholt, 1986; Omholt, 1987b, 1987a; Lemke and Lamprecht, 1990; Kleinhenz et al., 1995; Broomhead and Sumpter, 2000). The models relating to honeybee clusters can be divided into two groups, depending on the underlying model assumptions. Models like that of Myerscough (1993) assumed rules for global behavior of the cluster, i.e., metabolic heat generation rate is a function of honeybee position in the colony and try to predict the profile of temperature inside the cluster. The second group, e.g., Basak et al. (1996) and Watmough and Camazine (1995) assumed rules for individual behavior of the honeybees inside the cluster, e.g., metabolic rate of heat generation assumed as functions of local temperature and density of clustering of honeybees, which are used to predict the behavior of the cluster. These models assumed that the honeybees making the cluster did not move or allowed for movement of honeybees as in Watmough and Camazine (1995) where they allowed the cluster to change its shape by assuming that honeybees move in direction of decreasing temperature (negative thermotaxis).

Of the existing modeling studies, Basak et al. (1996) is most useful to our investigation. They assumed the honeybee swarm to be of a given fixed shape (obtained from field observations) and modeled the cluster as a porous medium made up of honeybees and air. They solved the steady or unsteady heat conduction equation with a source term accounting for heat generated from metabolic activities of the honeybees and used a fixed value for effective thermal conductivity which was a function of porosity of the cluster as well as the thermal conductivities of honeybee and air. Convective loss to the ambient air was assumed from the perimeter of the cluster. The heat lost was computed using a fixed value of the heat transfer coefficient derived from the engineering heat transfer literature. The metabolic activity of the honeybees was assumed to depend on the local thermal conditions in their immediate vicinity only. The metabolic heat generation rate was assumed to be a function of temperature, fitted against data from indirect calorimetric experiments in Southwick (1991). The temperature distributions computed within the cluster at different outside air ambient temperatures were in good agreement

with measurements of Heinrich (1981b). However, their model predicted results deviated from experimental measurements at higher ambient air temperatures, $> 15^{\circ}\text{C}$. This they explained (see Appendix in Basak et al., 1996) could have been caused by increased convective flow through the cluster possible at higher ambient air temperatures which they had not accounted for in their model.

In contrast to the heat transfer models studying thermoregulation in clusters, modeling effort to understand heat transfer in brood thermoregulation is more recent. In a detailed theoretical and numerical study, Humphrey and Dykes (2008) solved the unsteady two-dimensional conduction equation for thermal energy in a small section of an idealized honey comb to simulate the effect of cell heating bees entering empty cells in the brood and warming up neighboring pupae. Humphrey and Dykes (2008) concluded that the size of thermal region of influence depends on the number of cell heating honeybees and their distribution. They estimated from their numerical results that the size for a single cell heating honeybee is around 2–3 cells while for five cell heating bees it is around 3–4 cells. It was also observed that the temperature distribution on the brood surface is influenced by the distribution of cell contents in and around the brood area. An asymmetric temperature distribution was obtained for an asymmetric distribution of cell contents with more empty air filled cells in the bottom region of brood area and more honey filled cells above the brood area. The asymmetry is attributed to the different thermophysical properties of air and honey. They observed that the circular band of pollen filled cells observed around the brood area (Camazine, 1991) reduced the magnitude of this vertical asymmetry. In addition, based on non-dimensional analysis, they concluded that convection and radiation are negligible modes of thermal energy transfer for the comb. Based on this last finding we constructed a temperature profile which we applied as a Dirichlet boundary condition on the comb surfaces underneath the different honeybee clusters present inside the beehive. This simplified the problem as it removes one from solving a conjugate heat and mass transfer problem were one would need to solve the thermal energy equations in both the comb (conduction equation with source as in Humphrey and Dykes, 2008) and air space inside the beehive at the same time along with the flow equations in the air space. Details of the approach adopted in our study to set this temperature profile on the comb surface are provided in Section 3.4.

1.5. Objectives of the study

Given that thermoregulation and ventilation are energy intensive activities essential for the overall well being of colony inside the beehive, it would be useful to understand how the activities of the honey bees drives the flow inside the beehive and between the beehive and the outside ambient air. In this study, with the aid of some simplifying assumptions, we make a first attempt to model the important heat and mass transfer interactions inside the beehive and simulate the flow inside a beehive. In this regard, to best of our knowledge we are unaware of any earlier modeling study that has attempted in a systematic fashion to model a complete beehive (earlier models restricted to one cluster of honeybees) with a honeybee colony along with its brood present inside it during the early spring/summer season (earlier model dealt with honeybee cluster in winter when usually brood is not present inside the beehive). In view of these many firsts in this work, the tasks accomplished in this paper can be broken into two stages, first dealing with geometric model and simulation setup and second dealing with running simulations to answer interesting and important questions.

The objectives of our study are (a) systematically analyze the field data in the form of photographs we collected and use it to understand how the honeybees and comb contents are distributed inside the beehive, (b) use this understanding to develop a simple, parameterizable 3-D geometric model of the beehive with its contents, (c) develop a modeling framework that captures the relevant activities of the honeybees which serve as drivers for the flow inside the beehive, (d) to numerically solve the flow and energy transport equations in the air space in the beehive and understand quantitatively and visually how the flow inside the beehive changes as the outside air temperature is raised from 15°C to 30°C , this simulating usual late spring and summer conditions in temperate localities when brood rearing and honey flows are maximal, and (e) improve our understanding of how ventilation (i.e., removal of by products of metabolism) is accomplished by the honeybee colony with a brood at lower ambient air temperatures when we know fanning is not active, i.e., answer the important question “How honeybees engaged in brood thermoregulation activities which involve increased metabolism drive out the by products—namely carbon-dioxide and water vapor that result from this increased metabolic activity?”.

2. Preliminary considerations

2.1. Geometry of a Langstroth hive

The beehive considered in this study is called the Langstroth hive named after its inventor (U.S. Patent 9300, 1852). A typical hive, as depicted in Fig. 1, consists of a bottom board, on which boxes with the same rectangular cross-sections but possibly different heights are stacked. The bottom board that has a 2 cm high rim along three sides, on which the boxes sit, and an opening in the front which acts as an entrance allowing the honeybees to enter and leave the beehive. It also extends 5 cm in front of the boxes to provide a landing board for the honeybees. The hive body consists of rectangular wooden boxes without top and bottom. The lower boxes, called brood chambers, are placed first on the top of the bottom board. They contain the brood area of the beehive on its frames. The boxes, called honey supers which can be either deep or shallow in height, are placed on top of the brood chamber, from which they are separated by a wire mesh called the queen excluder, which keeps the queen honeybee in the brood chamber prevents her from laying eggs in the honey supers. A normal beehive during summer consists of one or two brood chambers and any where from one or ten honey supers.

Brood chambers and honey supers have removable frames (see Fig. 2(a)) which are supported on notches running in the front and back faces of the hive body near the top. The Langstroth beehive design provides the beekeeper an option to remove the frames individually to inspect the health of the brood, collect honey from the super frames, and to tend to damaged frames without disturbing the bee activities in the rest of the hive. This feature is believed to be one of the primary reasons responsible for the universal appeal, longevity (~ 150 years) and popularity of the Langstroth beehive. Each frame contains a foundation made of wax impacted with hexagonal ridges, called the comb surface. This is where the honeybees construct the characteristic hexagonal shaped cells using bee wax that they secrete. The queen bee resides in the brood chamber and lays eggs into the cells of the comb. Subsequently the worker bees cap these cells with developed pupae or cured honey using bee wax. The combs on the honey super function as a storage space for nectar/honey collected by the bees. During summer, the combs in the supers may fill with honey quickly and the beekeepers frequently remove the honey super to replace them with an empty one.

Commonly used Langstroth hives have 8–12 frames which are oriented such that the comb surfaces are perpendicular to the inlet at the bottom board. The frames are separated by a uniform

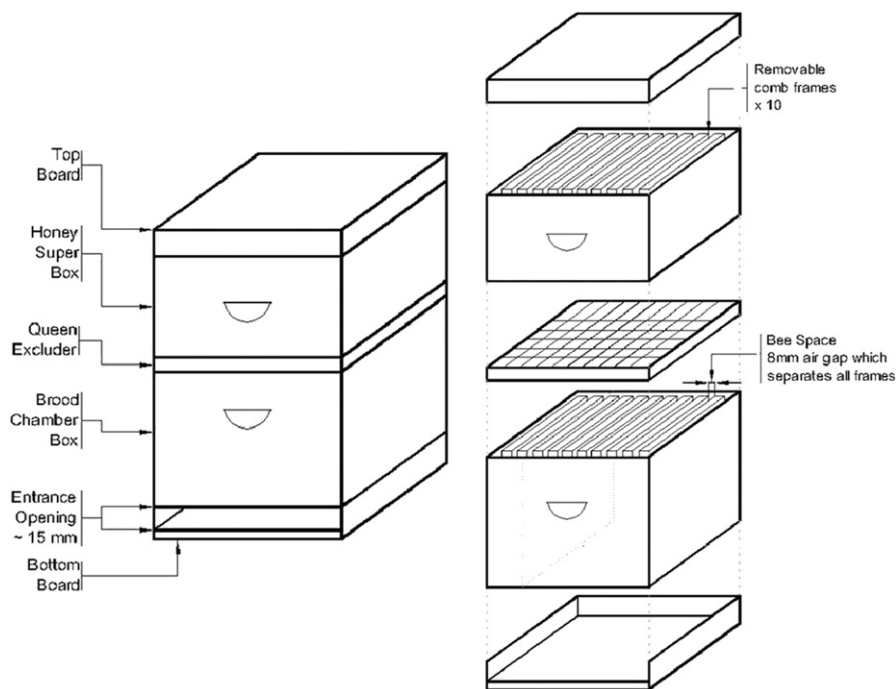


Fig. 1. Schematic of the Langstroth Beehive with one brood chamber and one honey super. The sketch to the left shows the beehive as seen from outside while to the right shows it opened up to show the 10 removable frames in super and brood chamber all separated by uniform spacing referred to as bee space ($3/8$ in).

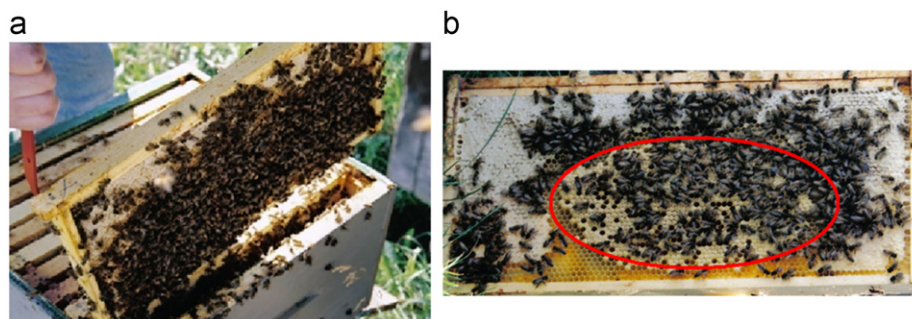


Fig. 2. Pictures showing (a) removable frame of a beehive brood chamber showing the cluster of bees sitting on the comb, (b) location and shape of brood (enclosed by a red line) and the honey area on a comb surface on a frame near the end wall of the beehive along the span. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

distance referred to as “bee space”, between 4.5 mm and 8 mm apart. Any spacing less than 4.5 mm causes the honeybees to glue the two opposite combs together while larger spaces more than about 8 mm are filled by the bees with wax comb. The intermediate spacing remains open and available as traffic channels for the honeybees. We assume in our model a bee space value of 8 mm. A original Langstroth beehive had only one inlet, located at the bottom of the brood chamber. In practice, many beekeepers over the years have modified the design to include additional openings. The role of these modifications in ventilation is a source of major debate in the beekeeper community. In our current first investigation, we assume a standard Langstroth hive with a closed top cover with only one inlet at the bottom.

2.2. Distribution of comb contents and honeybees in a hive

The first task in our modeling effort is to understand how the different contents of the beehive are distributed spatially inside the beehive. The contents of the beehive can be divided into two groups, the first one consisting of the contents that occupy the hexagonal cells in the comb (air in empty cells, pollen, brood, honey and cell

heating honeybees) and the second one consisting of the honeybees that occupy the air space between the comb surfaces.

To understand the spatial arrangement of hive content, we conducted periodic visual examination of beehives maintained at the University of Guelph’s Honey Bee Research Center at Townsend House during the summers of 2007 and 2008. The visual inspection was conducted by lifting the honey super of the top of the brood chamber and then observing the shape and size of the honeybee clusters between different frames in the brood chamber as seen in Fig. 2(a). Furthermore, weekly throughout the season (early spring to end of fall) all the comb surfaces in the brood chambers of two beehives were photographed, using a procedure similar to that explained in Knoop et al. (2006). In addition to our own visual inspection, we collected data from local beekeepers through a survey in which they were asked to sketch the shape of the honeybee clusters in their beehives over the course of a season. From analyzing the data from these two sources, the following observations were made namely:

1. **Brood shape and location:** The brood area on combs near the center of the beehive reflected a characteristic pattern of brood,

pollen, and honey consisting of three distinct regions—a central brood area, a surrounding rim of pollen, and a surround it a large peripheral region of honey. This is in agreement with the observations described in Seeley (1995), Winston (1987), Seeley and Morse (1976). In Camazine (1991), it was concluded from simulations that this pattern evolves from the self-organization, i.e., from the dynamic interactions among the processes of depositing and removing brood, pollen and honey, without a plan specifying spatial relationships. Fig. 2(b) shows the location of the brood and its contents on a comb surface on a frame away from the center of the beehive during one of our inspections. The brood area seen in Fig. 2(b) is shaped like an ellipse with the major axis along the length of the comb and minor axis along the height. The capped brood area is enclosed almost all the way around (except some portion along the bottom edge) by honey area and empty cells. The center of the ellipsoidal brood area is offset horizontally towards the beehive inlet. Furthermore, the ellipsoidal brood area is also shifted slightly towards the bottom edge of the comb as observed in Seeley (1983). The location and size of the brood area on the comb surfaces in adjacent frames facing each other was more or less identical. The comb surfaces on the first and last frames which face the end walls normally did not support a brood but had comb cells filled with capped honey.

2. *Seasonal variation of brood area:* During the course of an active beekeeping season starting from early spring to the end of fall, the conditions inside the beehive are in a state of constant flux. The strength of the bee colony (number of bees) changes and this change is often accompanied by changing shape, size and location of the brood area on the comb surfaces. In the beginning of the active season, the center of the brood area is closer to the inlet and its shape is elongated along the vertical direction. During the course of the season, as the size of the brood increases it gains a shape closer to the one seen in Fig. 2(b). In addition to this seasonal change, with the two weeks average incubation needed for the pupae to hatch into young worker honeybees, the distribution of empty cells and capped pupae in the brood area change continually.
3. *Brood area variation along span:* The shape, size and location of the brood areas on the two comb surfaces on adjacent frames facing each other is more or less the same. The brood area on the combs in the different frames decreases as one moves (Fig. 1) from the frame near the center towards the frame near the end walls. This variation of brood area along the X direction in Fig. 1 is seen to be more or less symmetric about

the YZ mid-plane (coordinate system as seen in Fig. 1), which divides the beehive into two equal halves.

4. *Distribution of honeybee colony inside a beehive:* The honeybee population in the beehive is mostly confined to the brood chamber. The cluster of honeybees in the bee-spaces between adjacent frames (referred to henceforth as bee cover volume or bee cover) is visible in the top view shown in Fig. 2(a). The variation in shape and size of the bee cover volume as we move along the span of the beehive plays an important role in driving the fluid flow inside the beehive. In the literature, to our best knowledge, the shape of the bee cover volumes and how the honeybees are distributed amongst the different bee covers between frames has not been carefully documented. The bee cover volume in the bee-space between adjacent frames is centered around the brood area and covers a greater area of the comb surface than the brood on frames. The size of the bee cover volume varies along the span (X direction in Fig. 1) of the beehive in just the same way as the brood area, i.e., it decreases from the bee-space in the center of the beehive towards the end walls.

2.3. Model reconstruction of a beehive

Based on our observations, a 3-D geometric model of a beehive and its content was constructed. An elaborate model that would treat all the honeybees inside the beehive individually was avoided as it can be cumbersome and instead each honeybee cluster was modeled as a fluid-saturated porous medium with the solid phase in it made up by honeybees and the fluid phase by air. Such an assumption treating the cluster as a porous medium has been used in the modeling work done in Basak et al. (1996) but without flow going through the porous medium. This approximation is valid due to the large number of honey bees present in each cluster and it provides a straightforward and simple way to accommodate interactions of the honeybees in an average sense, the exact details of how that is done are given in the next section.

Fig. 3(a) shows the isometric view of the model beehive used in our flow simulations. The model beehive has one brood chamber and one honey super. Both support eight frames which are uniformly spaced along the X direction, numbered 1–8. The eight frames in the brood chamber support seven honeybee clusters referred to in our discussion henceforth as bee cover volumes (shaded volumes in Fig. 3), numbered 1–7. On the first (#1) and last frame (#7) there is no bee cover volume on the comb surfaces

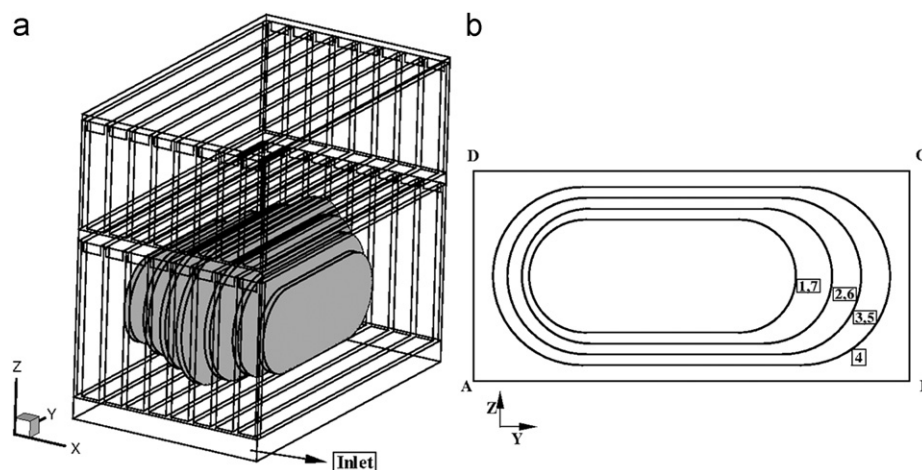


Fig. 3. The isometric view of the model beehive with eight frames with one honey super used in the simulations shown in (a) while the projection of the different bee cover volumes numbered 1–7 on the comb surface, where rectangle ABCD corresponds to the comb surface, shown in (b).

facing the beehive walls. The surfaces of the comb underneath each bee cover volume supports the brood. The size, shape and spatial variation of bee cover volume and the brood and the parameters used to characterize them in our model beehive are as follows:

1. *Bee cover volume shape and size*: The cross-section of each bee cover volume is assumed to have a shape consisting of a rectangle with two semi-circles at its vertical edges, see Fig. 2(a). This simplified shape was chosen because it closely resembled the shapes we observed during our inspections and because it is easily parameterizable. The size of each bee cover volume is characterized by specifying β_{bee} , which is defined as the percentage of the comb area covered by the bee cover volume and is given by

$$\beta_{bee} = \frac{A_{bc}}{A_{comb}} \times 100\% \quad (1)$$

where A_{bc} is the projected area of the bee cover volume on the comb surface and A_{comb} is the area of the comb surface. β_{bee} is a good measure to characterize the bee cover throughout the beehive as the comb area is constant in a given beehive as all the frames have the same size. The value of β_{bee} in the bee cover near the center of the beehive varies between 60% and 80%.

For our choice of the bee cover shape, the projected area of the bee cover volume is given by

$$A_{bc} = LW + \pi \left(\frac{W}{2} \right)^2 \quad (2)$$

where L, W are the length and height of the rectangle. For the center bee cover volume, given the value of β_{bee} and the area of the comb surface (fixed for a given frame size), we set the value of W to be 0.85 times width of the comb in Y direction (Fig. 3) based on our observations to obtain the value of L from (2).

2. *Span-wise bee cover volume variation*: The size of the brood decreases as we move from the comb surface near the center of the beehive towards the end wall. We conjecture that this spatial variation results from the time the single queen needs to move between the bee spaces to lay eggs in the brood areas, and the two weeks enclosing time of the pupae. Accompanying this brood size variation we can expect a proportional variation in the number worker honey bees needed to perform brood maintenance activities in each bee cover volume, i.e., the value of β_{bee} also decreases as we move from the center of the beehive towards the end wall. This variation in β_{bee} has been observed to be more or less symmetric about the midplane of the beehive along the span (X direction in Fig. 3). In addition to the reduction in value, the brood as well as bee cover volume in the bee spaces away from the center are also shifted slightly towards the inlet. The extent to which β_{bee} varies along the span has not been documented in the literature except getting briefly mentioned in Wedmore (1947).

In the current model, β_{bee} is assumed to vary linearly along the span of the beehive. Its gradient or variation is specified by fixing the values of β_{bee} at the center and near the end walls, $\beta_{gradient} = (\beta_{bee}^{center}, \beta_{bee}^{endwall})$. Based on our visual examination and from results of our survey, we observed that β_{bee} varied from around 60–80% near the center to as low as 30–50% in the bee cover near the end walls. We have fixed the size of the bee cover at the center of the beehive at 70% and studied the effect of span wise β_{bee} variation by considering different values for β_{bee} on the bee cover near to the end wall. For each $\beta_{gradient}$, the L and W for the off center bee cover volumes was set by assuming that the linear reduction in projected area of bee

cover volume was achieved by equal reduction in size of the bee cover in both directions, i.e., both L and W decreased equally and linearly.

3. *Brood area under bee cover volume*: The size of the brood, like the bee cover volume is characterized by β_{brood} defined as the percentage of the comb area occupied by the brood given by

$$\beta_{brood} = \frac{A_{brood}}{A_{comb}} \times 100 \quad (3)$$

where A_{brood} is area of the brood on each comb surface.

The value of β_{brood} can also specified by fixing the value of β_{ratio} , the ratio of brood area to projected area of the bee cover volume sitting over it defined as below,

$$\beta_{ratio} = \frac{A_{brood}}{A_{bc}}, \quad (4)$$

All bee cover volumes in the beehive occupy an area bigger than the brood areas they cover, i.e., $\beta_{ratio} < 1$. Based on our observations, the value of β_{ratio} was set to 0.3 and it was assumed to have same value for all bee cover volumes inside the beehive. The shape of the brood underneath each bee cover volume is assumed to be an ellipse with its center coinciding with the centroid of the rectangle. The major axis of the ellipse is oriented along the length of the frame (Y direction in Fig. 3). For a given value of A_{brood} , the values to use for the major and minor axis of the ellipse are chosen by setting the minor axis dimension to 0.5 W and calculating the major axis dimension.

A complete summary of the geometric parameters and the values assigned to them in the different simulations we did is given in Table 1.

3. Model formulation

3.1. Factors driving the flow

In the absence of wind outside the beehive, the flow in the beehive is driven by the density difference between the air inside the beehive and the ambient air arising due to honeybee activities inside the beehive. The driving mechanism for flow in such a case is either natural or mixed convection depending on whether the honeybees are engaged in fanning.

The summary of the different processes included in our model is given below:

1. *Heat and mass transfer from comb surfaces*: A fraction of the heat transferred to the brood by the brood thermoregulation efforts is lost to the air inside the beehive. To account for this heat transfer, we avoided solving the full conjugate heat and mass transfer problem but chose an approximate but simpler setup. A temperature profile which mimics the comb surface temperature that would arise from solving the comb energy equation as was obtained in Humphrey and Dykes (2008) was applied as a Dirichlet boundary condition for the fluid side energy equation on the walls of the comb surface underneath each bee cover volume. The details of the temperature profile construction are provided in Section 3.4.
2. *Heat and mass transfer to and from honeybees*: Honeybees derive energy to maintain their body temperature and perform activities predominantly by oxidizing glucose in the form of honey. This oxidation reaction is represented by the stoichiometric equation:



Table 1

Values of different geometric and boundary conditions related parameters used in the model.

Parameters	Values assigned
Width, height, thickness of frame	450 mm, 225 mm, 26 mm
Bee space, Inlet height	8 mm, 30 mm
$\beta_{\text{gradient}} \cdot \beta_{\text{brood}} \cdot R_{\text{active}}$	70–30 or 70–50; 0.3; 0.6
ϕ	0.4, 0.45, 0.5
T_{amb}	From 17.5 °C to 27.5 °C
Composition of inlet air	$Y_{\text{CO}_2} = 0.0$, $Y_{\text{H}_2\text{O}} = 0.0$, $Y_{\text{O}_2} = 0.22$, $Y_{\text{N}_2} = 0.78$
Comb wall temperature (T_{cw})	Uniform (33 °C or 36 °C), nonuniform (33–38 °C)
Honeybee size	$D_{\text{bee}} = 3$ mm, $L_{\text{bee}} = 11$ mm
ρ	Incompressible ideal gas mixture (19)
k_f, μ	0.0242 W/m·K, 1.8444e–05 kg/m s
$D_{\text{H}_2\text{O}}, D_{\text{CO}_2}, D_{\text{O}_2}, D_{\text{N}_2}$	2.88e–5, 1.60e–5, 2.0e–5, 2.64e–5 (units: m ² s ^{–1})

which results in mass exchange with the air, i.e., oxygen is consumed and water and carbon-dioxide are produced. The reaction is exothermic. Some of the heat released is used by the honeybees to maintain body temperature, another significant portion of this energy is lost as heat to the air, which drives the natural convection flow inside the beehive. The rate at which heat is generated by this metabolism of glucose is referred to as metabolic heat generation rate, usually specified per honeybee (G_{bee}) or per unit weight of the honeybee (G_{bee}). Humphrey and Dykes (2008) in their modeling work evaluated G_{bee} by solving the energy equation for a single honeybee assuming a nominal value for the temperature difference between the body of the honey bee and the air in its vicinity and for heat transfer coefficient. In our study, experimentally available values of G_{bee} were used and the details of how it was incorporated into our porous medium model is as explained in Section 3.5.

3. *Bee colony thermoregulation mechanisms*: The honeybees are not passive sources or sinks of heat and mass, but actively control their immediate local thermal environment individually, as well as a group by maintaining or raising their body temperature. This ability of individual honeybees to thermoregulate is important for the purpose of flight (Esch, 1976; Coelho, 1991; Roberts and Harrison, 1998) and for brood thermoregulation (Bujok et al., 2002; Kleinhenz et al., 2003). The nature of brood thermoregulation depends upon whether the ambient temperature is above or below the acceptable temperature range. The active response mechanisms affect the bees' metabolic heat generation rate. The resulting heat and mass exchange with the air affects the fluid flow inside the beehive. Furthermore, honeybees actively respond to increased humidity and increased carbon-dioxide concentration in the hive (Human et al., 2006; Seeley, 1974). A mathematical model for the fluid flow in a beehive that is valid over a wide range of ambient temperature conditions, needs to account for those effects. We are interested in an ambient air temperature range between 15 °C and 30 °C. In this range, only the brood warming thermoregulation activities are expected to be active, but not the brood cooling through evaporative cooling and beehive fanning. We do not treat the thermoregulation activities explicitly, but implicitly through the dependence of metabolic heat and mass generation rate on the activity level and through the temperature profile we apply on the comb surface underneath each bee cover volume.

3.2. Model assumptions

1. Wind outside the beehive is assumed to be negligible. The temperature of the air outside the beehive varies over the

days and nights during the summer and fall. However in our current investigation, for each simulation we fix the value of the outside air temperature (T_{amb}). The flow is simulated for different T_{amb} values between 15 °C and 30 °C. The effect of solar radiation entering the beehive through the hive inlet is neglected.

2. All the honeybees in the beehive are assumed to occupy the space between the comb surfaces in the brood chamber. The effect of the movement of the bees on comb surface, between bee cover volumes and from inside and outside of the beehive on the flow is not explicitly accounted for in the model. However, the activity level chosen while calculating metabolic heat generation rate accounts for the movement implicitly.
3. Inside the range of ambient air temperatures investigated in this study, only brood heating mechanisms via cell and surface heating honey bees and clustering are expected to be active and both these effects are included in our model.
4. A Dirichlet boundary condition is applied for temperature (see assumption #9) on the comb surfaces underneath each bee cover volume in the brood chamber. The comb surfaces in the brood chamber not under the bee cover volumes and the ones in honey super are assumed to be insulated.
5. Honeybee metabolism expressed in stoichiometric equation (5) is exothermic and involves mass transfer. The extent to which the mass transfer affects the flow inside the beehive is not known a priori and often studies of ventilation in human and animal habitats (Campen and Bot, 2003; Ould Khaoua et al., 2006; Chung et al., 1998; Norton et al., 2007) neglect the effect of mass transfer on the flow. In the case of a beehive, with several thousands of honeybees, the mass transfer can play a crucial role in directing the flow. This was confirmed from initial simulation studies (results not discussed here in) in which we compared results of these two studies – one where mass transfer effects were included and other not included. Therefore for all the simulations reported in this study, the density of the air was assumed to be a function of both temperature and concentrations of the different constituents that make up the air namely carbon-dioxide, water vapor, oxygen and nitrogen. The details of the equation of state assumed for air are provided in the next section on governing equations.
6. The bee cover volume is modeled as a fluid saturated porous medium in which honeybees represent the solid phase and air represents the fluid phase. The heat and mass transfer interactions of an individual honeybee inside the bee cover volume is captured via the different source terms in the energy balance equations written for the porous medium (Section 3.3).
7. Each cluster is modeled with a constant porosity and for most simulations except for some runs in case C the same porosity value was used for all the bee covers inside the beehive. The use of constant porosity inside each bee cover is an assumption we are forced to make as we found no easy way to ascertain during our visual examination of the beehive the number of honeybees in each cluster and their distribution, variables that we would need to ascertain porosity distribution in each cluster (see Section 3.5.1). This being a first full beehive model study, we restricted our self to modeling with constant porosity. However, with the availability of porosity distribution data in the future it can be easily incorporated into the current model.
8. The metabolic heat generation rate at any location in the bee cover volume is assumed to depend on the air temperature and the activity level of the honeybees. In addition, the metabolic heat generation is assumed to be constant in time.

9. Experimental observations of brood thermoregulation indicate that the cell heating honeybees warm up their thorax and dissipate the heat to the brood by spending an average of 10 min in the empty cells among the brood (Bujok et al., 2002; Kleinhenz et al., 2003). It is reasonable to assume that the cell heating bees on each comb surface behave independent of the cell heating honeybees in the other comb surfaces, deciding how often to reheat themselves and how long to stay in the empty cells in response to the rate at which the comb surface temperature drops due to heat loss. This lack of coordination between cell heating bees in different comb surfaces would result in each of these comb surfaces having their own unsteady temperature profiles. This being a first study, to model such a situation effectively we assume a comb surface temperature underneath the bee cover that volume is not a function of time. The spatially varying temperature applied on the comb surfaces below the bee cover volumes can be thought of as a time average of the actual unsteady comb surface temperature. In addition, we assume zero flux conditions for all species (carbon-dioxide, water vapor, nitrogen and oxygen) on all the comb surfaces in the brood chamber and honey super.
10. The net amount of heat transferred to the air from the honeybees and other hive contents is expected to be small. We therefore assume the resulting flow to be laminar. Moreover, since the assumed boundary conditions are also constant in time we solve for the flow using a steady state solver. To verify that the flow is indeed steady, additional a posteriori tests were performed as outlined later in Section 4.1.
11. In most applications involving heat transfer in a porous medium, the two phases – solid and fluid are assumed to be in thermal equilibrium. In such a case, a single energy equation including contributions from both phases is sufficient. However in our case, the honeybee body temperature is expected to be higher or lower than that local air temperature, i.e., we have no thermal equilibrium and need two energy equations, one for the fluid phase and another for the bee phase. In our case, although we assume no Local Thermal Equilibrium (LTE) approach, because of simplifying assumptions we make in the energy equation for the honeybee phase an assumption also employed in Humphrey and Dykes (2008), it reduces into a simple form which can be collapsed into the energy equation for the fluid phase. The details of this are provided in Section 3.3 while describing the governing equations.
12. The effect of humidity of the ambient air on the flow inside the beehive is not included in the model. The ambient air entering the beehive is assumed to be dry with no concentration of water vapor. The process of converting nectar stored in the honey super to honey involves evaporation to remove excess moisture from nectar as nectar contains more than 70% moisture while honey only around 20%. This being the first study and with lack of proper way to estimate rate of curing of honey, the flux of water vapor at the comb surfaces in the honey super corresponding to this curing process is neglected, i.e., assumed to be zero. This assumption implies that all the honey containing comb cells in the super are assumed to be capped. In addition, we assume that condensation of water vapor is negligible and that all the water remains in its vapor form in the air mixture.

3.3. Governing equations

The natural convection flow inside the beehive (partially porous enclosure) is modeled using a Darcy–Brinkmann–Förchheimer

equations based on a one-domain formulation. In this one domain formulation, a single set of governing equations valid for both porous and nonporous domains is used and the equations for the fluid domain are obtained automatically by setting a value of porosity $\phi = 1$. The one domain formulation avoids the requirement of internal boundary conditions at the fluid–porous medium interface. The validity of this one domain formulation in comparison with a two domain formulation was verified by Gobin and Goyeau (2008), who concluded that provided sufficient care is taken in the numerical approximations, both approaches lead to similar results for the simulation of heat and fluid flow in fluid–porous domains.

The following set of equations govern the mass, momentum, heat and species transport in the porous medium with no thermal equilibrium between the solid and fluid phases in the porous medium (Nield and Bejan, 2006; Pop and Baytas, 2002; Baytas, 2003; Liaqat and Baytas, 2001; Suzuki and Muralidhar, 2001):

Continuity equation:

$$\nabla \cdot (\rho_f \vec{v}) = S_m \quad (6)$$

where: ρ_f is density of the air mixture in kg/m^3 ; $\vec{v}$ is the velocity vector in m s^{-1} ; ∇ is the divergence operator in m^{-1} , and S_m is the source or sink term for mass generation in $\text{kg/m}^3 \text{ s}$ which has non-zero value only inside bee cover volumes due to honeybee metabolism given by chemical reaction in (5).

Momentum equation:

$$\nabla \cdot (\rho_f \vec{v} \vec{v}) = -\nabla p + \nabla \cdot (\vec{\tau}) + \rho_f \vec{g} + \vec{S} \quad (7)$$

where p is the static pressure in Pa; $\vec{v} \vec{v}$ is the dyadic product, $\vec{\tau}$ is the stress tensor in Pa; $\rho_f \vec{g}$ is the gravitational body force in N m^{-3} ; $\vec{S}$ is the external body force in N m^{-3} in which we include all other model-dependent source terms such as resistance to flow offered by porous media. The stress tensor $\vec{\tau}$ is given by

$$\vec{\tau} = \mu((\nabla \vec{v} + \nabla \vec{v}^T) - \frac{2}{3} \nabla \cdot \vec{v} I) \quad (8)$$

where μ is the dynamic viscosity in Pa s; T is transpose operator; I is the unit tensor, and the second term on right-hand side is the effect of volume dilation.

The source term $\vec{S}$ with cartesian components S_j describes flow resistance of the porous medium. It vanishes in the air phase. In the bee cover volumes it is determined by a combination of viscous surface friction and form drag forces. We use the Darcy–Förchheimer expression (Lage, 1998)

$$S_j = -\left(\frac{\mu}{K} + C_2 \frac{1}{2} \rho_f v_{\text{mag}} v_j\right) \quad (9)$$

where v_j are the velocity components in x, y, z directions in m s^{-1} and v_{mag} is magnitude of the velocity in m s^{-1} . The parameters K and C_2 are the permeability of the porous medium in m^2 and internal resistance in m^{-1} . They depend on the geometrical shape of the porous medium solid phase, its surface roughness, the porosity (ϕ) of the porous medium and the particle effective diameter d_p . The effective particle diameter d_p (Gaskell, 1992) is defined as

$$d_p = \left(\frac{6V_{\text{bee}}}{\pi}\right)^{1/3} \quad (10)$$

where V_{bee} is the volume of a worker honeybee. A worker honeybee is assumed to be a cylinder with length of 11 mm and diameter of 3 mm as suggested in Basak et al. (1996).

Assumed that honeybees are smooth particles, we use the Ergun (1952) equation to obtain the parameters as

$$\frac{1}{K} = \frac{150(1-\phi)^2 \lambda^2}{d_p^2 \phi^3} \quad (11)$$

$$C_2 = \frac{3.5(1-\phi)\lambda}{d_p\phi^3} \quad (12)$$

where ϕ is the porosity of the medium and λ is shape factor (Gaskell, 1992) given by

$$\lambda = \frac{A_{bs}}{\pi d_p^2} \quad (13)$$

where A_{bs} is the surface area of a honeybee in m^2 . In the air phase, $\phi = 1$.

Energy equation for the fluid phase:

$$\rho_f(c_p)_f \vec{v} \cdot \nabla(T_f) = \phi \nabla \cdot (k_f \nabla T_f) + h a_{sf}(T_{bf} - T_f) \quad (14)$$

where $(c_p)_f$ is the specific heat capacity of air in KJ K^{-1} ; k_f is thermal conductivity of air in $\text{W m}^{-1} \text{K}^{-1}$; T_f is air temperature in K; T_{bf} is local bee phase temperature in K; h is heat transfer coefficient at the air–honeybee interface and a_{sf} is specific surface area of the honeybee phase in the porous medium (surface area per unit volume of the honeybee).

Energy equation for the honeybee phase:

$$(1-\phi) \nabla \cdot (k_{bf} \nabla T_{bp}) - h a_{sf}(T_{bp} - T_f) + (1-\phi) q''_{bp} = 0 \quad (15)$$

where k_{bf} is thermal conductivity of the honeybee, T_{bf} is local honeybee phase temperature in K; and q''_{bp} is the metabolic heat generation rate by the honeybee per unit volume of the honeybee in W/m^3 . The last term in the energy equations for the fluid and solid/bee phase which appears with opposite signs in both these equations represents the heat transfer between the honeybee phase and air in its vicinity.

We assume that the conduction inside the honeybee phase represented by the first term in (15) is negligible compared to the other two terms. This allows us to drop the conduction term and we can collapse the honeybee phase energy equation into the fluid phase energy equation and rewrite the energy equation of the fluid phase as

$$\rho_f(c_p)_f \vec{v} \cdot \nabla(T_f) = \phi \nabla \cdot (k_f \nabla T_f) + (1-\phi) q''_{bp} \quad (16)$$

Species transport equation:

$$\nabla \cdot (\rho_f \vec{v} Y_i) = -\nabla \cdot (J_i) + S_i \quad (17)$$

where Y_i is mass fraction of species i in the air mixture and J_i is diffusion flux of species i in $\text{kg m}^{-2} \text{s}^{-1}$, given by

$$J_i = -\rho_f D_{if} \frac{\partial Y_i}{\partial x_i}, \quad (18)$$

where D_{if} is diffusion coefficient of the species i in the air mixture; S_i in (17) is a source or sink term in $\text{kg m}^{-3} \text{s}^{-1}$ due to the honeybee metabolism, which has a nonzero value only inside the bee cover volumes. A constant value is used for the diffusion coefficient of the different species.

Equation of state for air: The air is assumed to be an incompressible ideal gas mixture made up of the constituents carbon dioxide, water vapor, oxygen and nitrogen. The density of this mixture (ANSYS Inc., 2006) is calculated by expression:

$$\rho_f = \frac{P_{op}}{RT_f \left(\frac{Y_{CO_2}}{M_{CO_2}} + \frac{Y_{O_2}}{M_{O_2}} + \frac{Y_{H_2O}}{M_{H_2O}} + \frac{Y_{N_2}}{M_{N_2}} \right)} \quad (19)$$

where P_{op} is the operating pressure in Pa; R is universal gas constant in J/kg mol K ; T_f is temperature in K; Y_{CO_2} , Y_{O_2} , Y_{H_2O} , Y_{N_2} and M_{CO_2} , M_{O_2} , M_{H_2O} , M_{N_2} are the mass fraction and molecular weight (in $\text{kg}/(\text{kg mol})$) of the various air constituents.

The numerical values of the different input parameters used in the governing equations are given in Table 1.

3.4. Boundary conditions

To solve the governing equations boundary conditions must be specified. For the momentum equation, no-slip conditions ($\vec{v} = 0$) are specified along the hive walls and on all frame surfaces. Along the inlet to the beehive located at the bottom of brood chamber, pressure inlet boundary conditions were applied. The treatment of pressure inlet boundary conditions by the CFD software can be described as a loss-free transition from stagnation conditions to the inlet conditions. For incompressible flows, this is accomplished in Fluent[®] by application of the Bernoulli equation (ANSYS Inc., 2006).

For the species transport equations, we apply zero flux boundary conditions on the beehive walls and on the frames. This assumption is valid as the metabolic heat generated by the pupae in the brood and the mass flux of the different species accompanying brood metabolism is negligible in comparison to metabolic heat generated by the honeybees (Humphrey and Dykes, 2008; Stabentheiner et al., 2004; Lamprecht et al., 2005). Along the inlet, whenever flow enters the beehive, the value of species concentration is set to the concentration of the species in the ambient air, which we assume to consist of oxygen ($Y_{O_2} = 0.22$) and nitrogen ($Y_{N_2} = 0.78$).

For the energy equation, the inside walls of the beehive and the parts of the frames not covered by honeybees are assumed to be insulated. Dirichlet conditions are applied on the comb surface underneath the bee cover volume where the brood resides. To mimic the effect of brood thermoregulation by the worker honeybees we apply either a spatially uniform temperature of 33 °C or 36 °C or a spatially varying temperature on the brood surface. The former corresponds to an ideal situation where all of the brood is maintained at a constant temperature, while the latter is a more close to reality.

The spatially nonuniform temperature profile on the comb surface below bee cover volume is constructed based on experimental observations reported in Kleinhenz et al. (2003), Bujok et al. (2002) and on the numerical studies reported in Humphrey and Dykes (2008). Fig. 4(a) and (b) shows the temperature contours on the comb surfaces under the bee cover volumes #4 (close to center of beehive) and #1 (close to end wall of the beehive), for $\beta_{\text{gradient}} = 70-30$. Temperature contours shown in Fig. 4(a) and (b) divides the area under the bee cover into three regions. Region A has an elliptical shape and is enclosed by contour #6, region B envelopes region A and is enclosed by contours #1 and #6 respectively, region C is the remainder of the comb surface underneath each bee cover volume. Region A is the region where the worker honeybees actively engaged in brood thermoregulation. Its area is set to be 30% of the area of the comb surface underneath the bee cover as explained earlier in Section 2.3. A constant temperature of 38 °C is specified in region A, which is the steady state temperature value predicted in simulation studies of Humphrey and Dykes (2008) that would be established inside the brood region in the presence of cell heating bees. The region B, which envelops the region A all around, is the area over which the temperature control exerted by thermoregulating mechanisms active in region A extends, i.e., thermal radius of influence. To capture the vertical asymmetry in the temperature profile due to distribution of comb contents observed in the simulation results of Humphrey and Dykes (2008), we varied the thickness of region B and set its value above the brood area to 8 cells and below to four cells and varied the thickness of region B in the intermediate regions between these two values smoothly as seen in Fig. 4. The temperature value in region C is set to 33 °C, which is the average value of temperature over the brood. In region B, the temperature is assumed to vary linearly in the direction normal to the ellipse from 38 °C used inside region A to 33 °C used in region C.

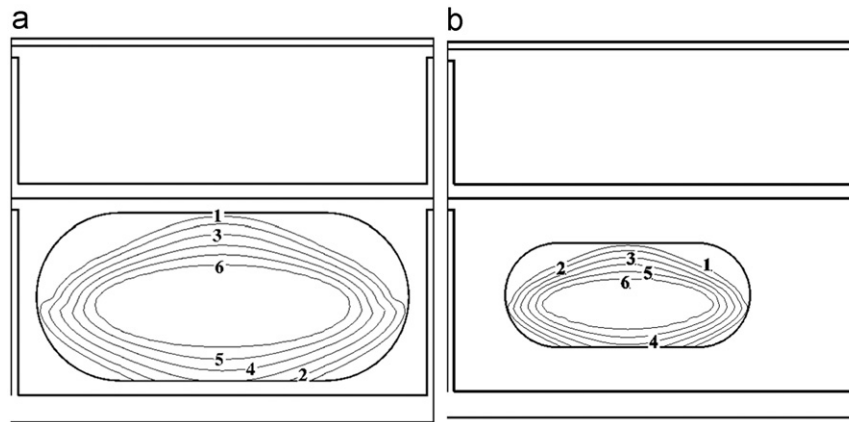


Fig. 4. Plots of temperature contours on one of comb surface underneath each of the bee cover volumes in a model beehive with β gradient = 70–30 where (a) is on the comb surface underneath bee cover volume #1 and (b) underneath bee cover volume #4. The contours 1–6 correspond to temperatures 33 °C, 34 °C, 35 °C, 36 °C, 37 °C and 38 °C respectively.

Fluent uses a semi-implicit iterative method to solve the governing equations, at the start of the iterative process, the initial value of the velocity for all cells is set to zero, the initial temperature set to 300 K, and the initial concentration of the different species is set to be same as their value in the ambient outside air.

3.5. Model parameters

3.5.1. Porosity of bee cover volume

Porosity in a fluid saturated porous medium is defined as the fraction of its total volume occupied by the fluid which in our case is air. If the spatial distribution of honeybees inside each bee cover volume is assumed to be uniform, the porosity ϕ of each bee cover volume can be calculated by

$$\phi = \frac{V_{air}}{V_{bc}} = 1 - \frac{V_{bee-phase}}{V_{bc}} \quad (20)$$

where V_{bc} is the total volume of the bee cover and $V_{bee-phase}$ is the total volume occupied by the honeybees present in it. If we assume all honeybees to have the same size and shape, the above equation can be rewritten as

$$\phi = 1 - \frac{N_{bc}V_{bee}}{V_{bc}} \quad (21)$$

where V_{bee} is the volume of a single honeybee, and N_{bc} is the number of honeybees present in a bee cover volume.

An estimate of the number of honeybees in each bee cover along with volume of each bee cover is needed to evaluate ϕ from (21). An approximate value to use for bee cover volume can be obtained from the shape of the bee cover volume seen during visual inspections, but an estimate of number of honeybees inside a bee cover volume or in the whole beehive is difficult to obtain via visual means. Earlier models studying heat transfer in winter clusters and honeybee swarms (Lonvik and Omholt, 1986; Omholt, 1987b; Broomhead and Sumpter, 2000; Lemke and Lamprecht, 1990) used either mass density of the honeybees or number of honeybees per unit volume as a variable instead of porosity. This worked well as the earlier models were primarily heat conduction models, neglecting the flow through the cluster. In Basak et al. (1996), studying heat transfer in honeybee swarms, an estimate of number of honeybees in a swarm given in Heinrich (1981b) was used to evaluate the porosity. In Watmough and Camazine (1995) studying a model of thermoregulation in honeybee clusters an estimate for the density provided in Heinrich (1981b) was used. The estimate suggested in Heinrich (1981b) was

2 bees per cm^3 at higher ambient air temperatures increasing to maximum of 8 bees per cm^3 at low ambient air temperature.

In our model, we use (21) to compute the porosity by substituting for V_{bee} the value computed by assuming the honeybee to be a cylinder with length = 11 mm and diameter = 3 mm (Basak et al., 1996) and for N_{bc}/V_{bc} the values of Heinrich (1981b). This resulted in $0.4 \leq \phi \leq 0.5$, which is the range of values for ϕ used in this study. The value of porosity is assumed to be same in all the bee cover volumes in our simulations, except for simulations done for Case C where it is varied from one bee cover volume to other.

3.5.2. Metabolic heat generation rate per unit volume of honeybee

Calorimetry experiments conventionally measure metabolic heat generation rate per unit mass of the honeybee (g_{bee} in Watts/kg) or per honeybee (G_{bee} in Watts). The metabolic heat generation rate per unit volume of the honeybee phase, q''_{bp} , needed in (16) can be calculated from G_{bee} or g_{bee} as

$$q''_{bp} = \frac{G_{bee}}{\pi(D_{bee}/2)^2 L_{bee}} = \frac{g_{bee}}{M_{bee}\pi(D_{bee}/2)^2 L_{bee}} \quad (22)$$

where L_{bee} and D_{bee} are the length and diameter of a honeybee modeled as a cylinder (Basak et al., 1996) and M_{bee} is the mass of a honeybee which varies from around 80 mg to 110 mg depending on the amount of honey stored in their honeysacs. In (22) we have assumed that the heat generation is distributed uniformly through out the volume of a honeybee.

The metabolic heat generation rate is measured in controlled experiments using direct calorimetry (Schmolz et al., 1995, 2001, 2002) or indirect calorimetry (Cahill and Lustick, 1976; Vollmann et al., 2003; Stabentheiner et al., 2004; Kovac et al., 2007). In direct calorimetry experiments, the temperature increase of the air at a given flow rate flowing over a honeybee or a cluster of honeybees held inside a controlled temperature environment is measured. From these experiments, the heat generation rate per unit weight of the honeybee, g_{bee} , is calculated, from which q''_{bp} can be calculated using (22). In indirect calorimetry, the change in concentration of carbon-dioxide or oxygen in air flowing at a given flow rate over cluster of honeybees held inside a controlled chamber is measured. These experiments report either the volume rate of oxygen consumption, $\dot{V}_{O_2}$, or volume rate of carbon-dioxide production, $\dot{V}_{CO_2}$, both expressed in $\mu\text{l}/\text{min}$ per honeybee measured at STP (Standard Temperature Pressure: $T=273\text{ K}$, $P=1\text{ Pa}$) conditions. q''_{bp} can be inferred indirectly after converting $\dot{V}_{O_2}$ or $\dot{V}_{CO_2}$ to G_{bee} , with the assumption that the combustion of honey is an aerobic process following the

stoichiometric equation given in (5). The three steps involved in the conversion process are

1. Convert $\dot{V}_{O_2}$ to the number of moles of O_2 consumed per unit time ($\dot{N}_{O_2}$) given that 1 mol of any gas occupies 22.4 L at STP.
2. Convert $\dot{N}_{O_2}$ to number of moles of glucose consumed per unit time $\dot{N}_{C_6H_{12}O_6}$ from stoichiometric Eq. (5), i.e., 1 mol of glucose needs 6 mol of oxygen.
3. Convert $\dot{N}_{C_6H_{12}O_6}$ to G_{bee} using that 1 mol (180 g) of glucose ($C_6H_{12}O_6$) produces 2874 kJ of energy.

The metabolic heat generated by honeybees has been found from experiments to depend on (a) activity level of the honeybee (Crailsheim and Stabentheiner, 1999; Kovac et al., 2007), (b) air temperature in the vicinity of the honeybee (Crailsheim et al., 1999), and (c) age and sex of honeybee (worker, drone or Queen) (Cahill and Lustick, 1976; Stabentheiner et al., 2004). Moreover, the metabolic heat generation rate obtained from experiments done with groups of honeybees indicate a lower value (10%) than obtained from experiments done with a single honeybee (Seeley, 1995). In honeybees with moderate and high activity, the metabolic heat generation rate decreased linearly with temperature. In resting or sleeping honeybees it increases with increasing temperature following a sigmoidal shape (Kovac et al., 2007), with the value for resting honeybee being orders of magnitude smaller than those for the active honeybees at all temperatures.

Two different approaches have been used in the earlier modeling work on heat transfer and thermoregulation in honeybees, a direct approach where experimentally measured or inferred values of metabolic heat generation rate were used, or an indirect approach like in Humphrey and Dykes (2008) where measured values of honeybee body temperature were used along with a value for heat transfer coefficient and honeybee surface area to evaluate metabolic heat generation rate. In models using the direct approach, the metabolic heat generation rate obtained from experiments have been considered as a constant or as a linear or quadratic function of temperature with negative slope (active honeybees) (Lonvik and Omholt, 1986; Southwick, 1991; Myerscough, 1993) or an exponential function using Q_{10} analogy (resting honeybees) (Omholt, 1987b).

In our study, the metabolic heat generation rate value at the centroid of each grid cell inside the bee cover volume is assumed to be a function of temperature of air and activity level of the honeybee at that location. The activity level of the honeybees involved in brood maintenance is specified by setting the value of

R_{active} , the ratio of total number of active honeybees to the total number of honeybees in the bee cover volume. We made the following assumptions: (a) the honeybees have one of two activity levels, active or passive like done in Humphrey and Dykes (2008), (b) the number of active honeybees in each bee cover is proportional to the size of the brood, (c) R_{active} is constant for all bee cover volumes inside the beehive. These assumptions ensured that the number of active honeybees assigned per unit projected area of the bee cover volume is held constant for all the bee cover volumes inside the beehive.

Inside each the bee cover volumes q''_{bp} needed in the governing Eq. (16) is evaluated using expression:

$$q''_{bp} = \beta_{corr}((1-R_{active})g''_{passive}(T) + R_{active}g''_{active}(T)) \quad (23)$$

where $g''_{active}(T)$ and $g''_{passive}(T)$ are the metabolic heat generation rates per unit volume of active and passive honeybees and $\beta_{corr} = 0.10$, is factor to used to correct experimental measurements made using single honeybee and make data applicable for a group of honeybees clustered together as was done in the modeling study reported in Basak et al. (1996).

Previous models of heat transfer in honeybee clusters during winter used different expressions to quantify the temperature dependence of metabolic heat generation rate, valid in the temperature range from -10 to 15°C . These did not explicitly account for the different activity levels of honeybees expected in the summer. Therefore, they cannot be extended to higher temperature ranges. In our study, the expressions $g''_{active}(T)$ and $g''_{passive}(T)$ were obtained from the indirect calorimetry experimental data given in Vollmann et al. (2003), where they measured oxygen consumption rate of honeybees ($\dot{V}_{O_2}$) in $\mu\text{L min}^{-1}$ per honeybee as a function of temperature at different activity levels. The $\dot{V}_{O_2}$ data showed a decrease with increasing temperature. We fitted linear functions ($r^2 = 0.92$) against the data to obtain the temperature dependance as

$$\dot{V}_{O_2}^{active} = A_{active} + B_{active}T \quad (24)$$

$$\dot{V}_{O_2}^{passive} = A_{passive} + B_{passive}T \quad (25)$$

Using the conversion process described earlier, the oxygen consumption rate expressed by the (24) was converted to obtain the source terms occurring in the energy and species transport equations. Fig. 5 shows plot of heat generated per unit volume of active and passive honeybees and mass generation rate of carbon-dioxide per unit volume of active and passive honeybees at different temperatures, the plots of mass generation rate of water

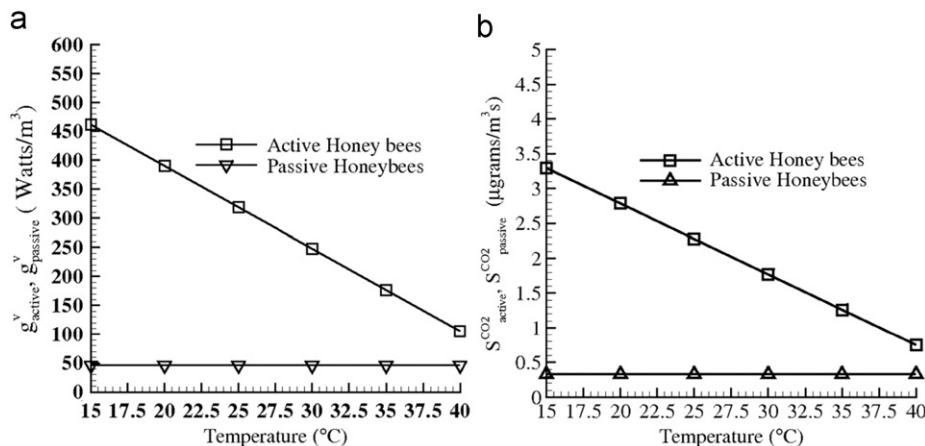


Fig. 5. Plots of quantities used to evaluate source terms in governing equations as function of temperature for both active and passive honeybees: (a) heat generation rate per unit volume, (b) mass of carbon-dioxide generated expressed per unit volume of a honeybee and per unit time.

vapor and consumption rate of oxygen look similar to carbon-dioxide and are not shown.

3.5.3. Source terms in species transport equations and continuity equation

The source term S_i (in $\text{kg/m}^3 \text{s}$) in the species transport equation (17), where i stands for either of CO_2 , H_2O , O_2 or N_2 , and the source term in the continuity equation S_m (6) are both related to q''_{bp} in the energy equation (14). This relationship is to be expected as the same honeybee combustion process that generates the heat is accompanied by consumption of oxygen and production of water vapor and carbon-dioxide, i.e., combustion of 1 mol (180 g) of glucose ($\text{C}_6\text{H}_{12}\text{O}_6$) produces 2874 kJ of energy in addition to producing 6 mol of water vapor and carbon-dioxide and consuming 6 mol of oxygen. Therefore a conversion factor can be worked out to compute the S_i terms once q''_{bp} has been obtained as a function of local temperature as explained in Section 3.5.2. To speed up the calculation, this conversion is performed outside the Fluent® UDF environment, i.e., we calculate the coefficients A_i and B_i , which appear in the linear *ansatz* for $S_i(T)$, i.e., $S_i = A_i + B_i T$, where T is the temperature of the air in centigrade (Fig. 5(b)–(d)).

The source term S_m in the continuity Eq. (6) is given by

$$S_m = S_{\text{CO}_2} + S_{\text{H}_2\text{O}} - S_{\text{O}_2} \quad (26)$$

It has a positive value inside each bee cover volume, i.e. net mass is added to the air due to combustion of honey.

4. Solution procedure

4.1. Numerical methodology

The governing equations (6), (7), (16), (17) are solved numerically using the commercially available Computational Fluid Dynamics (CFD) software package Fluent® (ANSYS Inc., 2006). Fluent uses a control-volume-based technique (Malalasekera and Versteeg, 1995) to convert the governing equations to algebraic equations that can be solved numerically. The control volume technique consists of integrating the governing equations about each control-volume that yield discrete equations that conserve each quantity on a control-volume basis. The discrete form of the conservation equations are solved using a Gauss–Seidel linear equation solver in conjunction with an algebraic multigrid method. Prior to discretization, a computational grid was obtained for the complete geometry using the GAMBIT grid generation software available with Fluent. The grid generation was performed carefully to guarantee that the key features of the flow are preserved in the numerical approximation. The details of grid generation and the efforts taken to ensure that the results are grid independent are explained in Section 4.2.

The source terms in the momentum, energy and species transport equations have a non-zero value only inside the bee cover volumes. The source term in the momentum equations modeled by (9) are included in Fluent by setting all the bee-cover volumes as porous zones and giving the value of porosity ϕ in each of them. The source terms in continuity, energy and species transport equations are provided as user-defined functions (UDF). Inside these UDF functions, the value of the source term for each equation in each control volume cell was evaluated based on the value of temperature of the fluid at the cell centroid using the formulation explained earlier in Section 3.5. The source terms included in the UDF code were linearized using the rules defined in Patankar (1980) to ensure that calculations were stable. The program's double precision segregated solver was used to solve the discretized equations.

The default porous medium model in Fluent® assumes Local Thermal Equilibrium (LTE) exist between the honeybee and the fluid phases that make up our saturated porous medium. In order to simulate no local thermal equilibrium approach (Assumption 11 see Section 3.2) between the honeybee phase and the fluid (NLTE approach) at each location inside the porous medium we set the solid phase material properties (conductivity, specific heat) in Fluent® default porous medium energy equation to zero. In addition as explained earlier we added the source term $((1-\phi)q''_{bp})$ to the energy equation added via UDF as explained earlier.

Fluent uses a collocated grid where the discrete values of different variables (u, v, w, P, T, Y_i) in each control volume are stored at the centroid of each cell. The face values of the variables needed to evaluate convective and diffusive terms when solving the equations using a control volume formulation are obtained by interpolation. The energy, momentum and species concentration variables needed at cell faces in the convective terms were found by using the Quadratic Upstream Interpolation for Convective Kinetics (QUICK) scheme (Leonard, 1991), while the central difference scheme was used to approximate the diffusion terms. The PREssure Stagging Option scheme (PRESTO) was used to find the pressure values at the cell faces. PRESTO is similar to the staggered grid approach described in Patankar (1980), and is recommended for buoyancy flow and hexahedral meshes. The Semi-Implicit Method for Pressure-linked Equations (SIMPLE) (Patankar, 1980) was used to model the coupling between the pressure and velocity. As the equations are nonlinear under-relaxation was used for the variables to avoid divergence.

For the range of values assumed for the different model parameters (T_{amb} , ϕ) in this study, the flow is expected to be steady and laminar (Assumption #10). Therefore, the governing equations are solved using a stationary solution procedure (i.e., no unsteady terms in the governing equations). To verify the validity of our steady state flow assumption and to ensure that the flow computed by the stationary solution procedure are not erroneous (i.e., steady state picture of an otherwise unsteady flow), two simulations were done using a transient solution approach. The unsteady version of the governing equations were solved using the PISO scheme and the values set for the different model parameters in these simulations were $\beta_{\text{gradient}} = (70, 30), (70, 50)$, $T_{amb} = 17.5^\circ\text{C}, 27.5^\circ\text{C}$ (the maximum and minimum values used in our study) and $\phi = 0.45$. For these two values of T_{amb} , the strength of the source term in energy Eq. (16) which predominantly drives the natural convection flow is expected to be maximum and minimum, because of the negative slope of the linear function fit used to represent the source terms as a function of temperature. The solution from the transient solution procedure for each of these four cases converged to a stationary solution and compared well with the solution obtained using the same parameter values with the stationary solution procedure on the same grid, thereby validating our assumption that the flow is steady. Therefore, for all the simulations for which results are reported in this study, only the stationary solution procedure was used to solve the governing equations.

Convergence, when using the stationary solver, was determined by checking the scaled residuals (ANSYS Inc., 2006) and ensuring that they were smaller than 10^{-5} for the continuity and velocity variables, smaller than 10^{-6} for the energy equation and smaller than 10^{-5} for the species equations respectively. In addition to monitoring the residuals, the volume averaged molar concentration of carbon-dioxide in each bee cover region and the net heat flux from each comb surface underneath the bee cover volumes were monitored. If the residuals meet their convergence criteria and the monitored quantities converged towards a constant value, we concluded that the simulation had reached a

steady solution. For the simulations done in this study, with the nominal value used for under-relaxation process, the convergence was achieved within 8000–10,000 iterations, which took on an average a wall clock time of 48–60 h. The computations reported in this study, were performed on the several distributed memory clusters provided by the Shared Academic Research Computing Network (SHARCNET) of which University of Guelph is a part. Most simulations were run in parallel mode, using 8 processors on a Hewlett Packard manufactured cluster with Myrinet interconnect.

4.2. Computational grid

To accurately simulate the 3-D flow inside the beehive a carefully constructed, sufficiently refined computational grid was generated. To ensure that we balance the competing concerns of computing speed and the need to resolve flow features, we chose the number of frames in our model beehive to be eight instead of nine or ten i.e. at the lower end of what is practically used in beehives.

The quality of the flow simulation results depends on the quality of the grid, therefore special care was taken to ensure that we have a high quality grid with good clustering of cells near the different boundaries (needed due to boundary layers) which at the same time was of a reasonable size that can be computed with the available resources. To achieve this goal, prior to the actual grid generation, a multi-block structure was adopted and the flow domain was divided into smaller volumes each of them predominantly hexagonal in shape. The structured grid generation techniques available in Gambit[®] was used to generate the grid first along the edges, then faces, and then in the various sub-volumes.

The grid independent study to arrive at the final grid used in our simulations was done in two steps, where in the first step we fixed the number of subdivisions to use along the different edges of the beehive while in the second step we fixed the fine grid resolution needed at the porous–nonporous interface and near the walls to resolve the boundary layers. In the first step, we solved a simpler problem of flow inside the beehive with no honeybees which is driven only by the temperature boundary condition (see Section 3.4) applied on the comb surfaces. In this setup, with the absence of honeybee metabolism inside the beehive, the species transport equations (17) were discarded and the coupled flow and energy equations (6)–(14) were alone solved along with the assumption of incompressible ideal gas equation of state for air. This greatly reduced the time needed to solve the problem enabling us to use this setup effectively to perform grid resolution studies. Based on this study, the number of grid nodes needed along the different edges of the beehive to resolve the flow was chosen. The grid was clustered such that the grid size was smaller next to all the solid surfaces inside the beehive to resolve the flow and thermal boundary layers. In the second step, the full heat and mass transfer problem was solved with honeybees present inside the beehive in a model beehive with β -grad of 70–30 and ϕ set to 0.45 at an ambient air temperature $T_{amb} = 17.5$ °C. By repeatedly refining the grid, the

grid clustering needed to resolve the boundary layers at the porous–nonporous interface was fixed. The total size of the final grid with this multi-block structure which we arrived at in the end of the grid dependence study was close to 2.5 million cells.

4.3. Parametric studies

To understand the influence of the model parameters, a systematic parametric study was conducted. Based on the parameter that is varied and for ease of presentation, the simulations done in this study are grouped into three cases labeled A and B and C. The values assigned for different model parameters and the boundary conditions used for each of the cases is as given in Table 2. In case A, we studied the influence of the temperature boundary condition applied on the comb surfaces underneath each bee cover volume. We investigated two scenarios, an idealized conditions where we applied a spatially uniform temperature of 33 °C or 36 °C and the other where we applied spatially nonuniform temperature on the comb surfaces. The details of spatial variation are as explained in Section 3.4. In case B, we tried to understand how the structure of the flow inside the beehive changes as we change the ambient air temperature (T_{amb}) and porosity of the bee cover volumes. For simulations in both cases, the porosity of each bee cover volume inside the beehive was set to the same value. In addition, in few simulations in case B, we investigated the effect of using different starting conditions for our iterative solver. In one scenario we started the simulations as described Section 3.4, in the other one we started with the steady state solution obtained with a lower or higher ambient temperature T_{amb} , e.g., using steady state result obtained using $T_{amb} = 22.5$ °C as a starting condition for the simulation where $T_{amb} = 25$ °C. In both cases the same final steady state solution was reached, moreover we observed that the latter choice did not reduce the computing time significantly.

In case C, to mimic varying conditions inside a beehive, we investigated the effect of varying porosity inside a beehive between bee cover volumes, however, keeping the porosity value constant inside each bee cover volume. For the purpose of brevity, only brief summary of conclusions from case C without providing any supporting figures is given in Section 5.3 and the corresponding figures for this case are provided as a part of the supporting material accessible online to the readers via the journal website.

4.4. Post-processed quantities

To understand the influence of different model parameters, we computed integral values of quantities over different regions inside the beehive. These quantities used in conjunction with conventional flow visualization techniques provided us an effective way to understand the salient features of the flow.

1. **Ventilation flow rate:** Ventilation flow rate (often expressed in L/min) is the measure of the rate of air exchange between the beehive and the outside ambient air. It can be quantified by

Table 2
Summary of parameters and boundary conditions used for the different parametric studies.

Case name	Parameters	Summary
Case A	$\phi = 0.45$, $\beta_{\text{gradient}} = 70-30$, $T_{amb} = 20$ °C, $T_{cs} = 33$ °C/36 °C/33–38 °C	Effect of uniform and nonuniform comb wall temperature on flow
Case B	$\phi = 0.4/0.45/0.5$, $\beta_{\text{gradient}} = 70-30/70-50$, $T_{amb} = 17.5-27.5$ °C, $T_{cs} = 33-38$ °C	Effect of varying outside air temperature on the flow inside the beehive
Case C	ϕ = varies in beehive (see Supporting material), $\beta_{\text{gradient}} = 70-30$, $T_{amb} = 20$ °C, $T_{cs} = 33-38$ °C	Effect of spatially varying porosity across bee cover volumes inside the beehive

specifying either the inflow rate or the outflow rate, where the inflow and outflow rate are defined as the volume of air entering and leaving the beehive per unit time. The volume inflow and outflow rate are given by

$$\dot{V}_{inflow} = \int_{\Omega_i} |\vec{v} \cdot \vec{n}| dA; \quad \dot{V}_{outflow} = \int_{\Omega_o} |\vec{v} \cdot \vec{n}| dA, \quad (27)$$

where $\vec{v}$ is the fluid velocity vector, $\vec{n}$ is the outward pointing normal to the inlet face and Ω_i and Ω_o are the regions of the inlet face over which the flow enters and exits the beehive respectively, i.e., $\vec{v} \cdot \vec{n} < 0$ over Ω_i and $\vec{v} \cdot \vec{n} > 0$ over Ω_o .

Inside each bee cover volume, as a result of the honeybee metabolism net mass is added to the air mixture, i.e., positive value for $S_m > 0$ the mass source term in (6). The S_m value summed up over all the bee cover volumes is small and the net effect of this on the difference between the computed inflow and out flow rate is small, i.e., $\dot{V}_{inflow} < \dot{V}_{outflow}$ but $|\dot{V}_{inflow} - \dot{V}_{outflow}|$ is small. Therefore in our presentation of results, we report only $\dot{V}_{inflow}$ value with the understanding that the corresponding $\dot{V}_{outflow}$ would be only slightly larger.

2. *Heat transfer related quantities:* The total heat generated per second (Q_{bc}^i) by the honey bees occupying each bee cover volume is

$$Q_{bc}^i = \int_{\Omega_i} (1-\phi)q_{bp}'' dv, \quad i = 1, \dots, 7 \quad (28)$$

where Ω_i is the volume of each bee cover volume and q_{bp}'' is the rate of heat generation per unit volume at each location inside the bee cover volume.

The net heat transferred per second to the comb surfaces (cs) underneath each bee cover volume is

$$Q_{cs}^i = \int_{cs} q_{cs}'' dA, \quad i = 1, \dots, 7 \quad (29)$$

where q_{cs}'' is the heat flux on the comb surface and integration for each i is done over both the comb surfaces that make up each bee cover volume.

The net heat lost to the air (Q_{net}^i) from each bee cover volume is

$$Q_{net}^i = Q_{bc}^i - Q_{cs}^i, \quad i = 1, \dots, 7. \quad (30)$$

We also computed the average body force in each bee cover volume

$$BF_{avg}^i = \frac{\int_{\Omega_i} (\rho - \rho_{ref})g dv}{V_{\Omega_i}}, \quad (31)$$

where V_{Ω_i} is the volume of the bee cover volume and the reference density ρ_{ref} is the density of the ambient air outside the beehive evaluated using (19) substituting $T = T_{amb}$ and $Y_{O_2} = 0.22$, $Y_{N_2} = 0.78$ and $Y_{H_2O} = Y_{CO_2} = 0$ respectively.

3. *Mass transfer related quantities:* Honeybee metabolism produces equal number of moles of carbon-dioxide and water vapor for each mole of honey consumed, as seen in (5). With the diffusivities of both carbon-dioxide and water vapor being of the same order of magnitude, the integral quantities computed using their respective concentrations inside the bee cover volumes will follow the same trend. In view of this, we present only carbon-dioxide related quantities. The total mass $M_{CO_2}^i$ and the mass generated per unit time $\dot{M}_{CO_2}^i$ of carbon-dioxide inside a bee cover volume

$$M_{CO_2}^i = \int_{\Omega_i} \rho Y_{CO_2} dv; \quad \dot{M}_{CO_2}^i = \int_{\Omega_i} S_{CO_2} dv, \quad (32)$$

where Y_{CO_2} is the mass fraction of carbon-dioxide and S_{CO_2} is the rate of carbon-dioxide generation per unit volume of the bee cover. The ratio of $\dot{M}_{CO_2}^i$ and $M_{CO_2}^i$ which has the units of time is referred to as pseudo-residence time, τ_i was also

computed for each bee cover volume. It is a measure of the convective flux through the, bee-cover volume with the larger values of τ_i indicative of a slower flow through the bee-cover and vice-versa. In addition, we also quantified the ability of the flow exiting the beehive to remove some of the carbon-dioxide produced inside the beehive, by calculating the carbon-dioxide clearance efficiency η_{CO_2} given by

$$\eta_{CO_2} = 100 \times \frac{M_{out}^{CO_2}}{\sum_i M_{CO_2}^i}, \quad (33)$$

where the numerator is the mass flux of carbon-dioxide out of the beehive and the denominator is the sum of mass of carbon-dioxide generated per second inside each of bee cover volumes present inside the beehive. In addition to the above mentioned quantities, the average concentration of carbon-dioxide in each bee cover was also calculated.

5. Results and discussion

5.1. Case study A: effect of brood thermoregulation on flow

The ventilation flow rate (figure not shown) did not show appreciable change in value when we varied the value of ϕ for the different comb wall temperatures (T_{cs}). We observed that ventilation flow rate at all ϕ values for 36 °C case was greater than that for 33 °C case by an average of 8–10% which was in turn greater than that for 33–38 °C case by around 2 to 5%. The carbon-dioxide clearance efficiency (η_{CO_2}) value (figure not shown) for all the cases varied in the range between 45% and 55%. In addition, we observed that as we varied ϕ , at each ϕ value, the η_{CO_2} for $T_{cs} = 36^\circ\text{C}$ case was greater than η_{CO_2} for 33 °C by an average of 10% while the η_{CO_2} for the 33–38 °C case was bounded between the values for two uniform T_{cs} cases. The η_{CO_2} for uniform T_{cs} cases changed little as ϕ was varied, while for η_{CO_2} for 33–38 °C showed a maximum value at $\phi = 0.45$.

The small separation space (~ 8 mm) between the frames and the reduced flow inside the honeybee clusters ensures that the temperature of the air at any location inside the cluster does not deviate much from the temperature on the comb surface next to it. We observed that for all T_{cs} cases we considered, the average temperature difference was less than or equal to 1 °C and the maximum difference in temperature was around 2–2.5 °C; with this maximum occurring only over a very small region of the bee cover at the bottom where the flow enters the bee cover volume from the space below the brood chamber. This observation coupled with negative slope in the linear function (function of T) used to model the different heat and mass source terms in the governing equations would result in Q_{bc} and $\dot{M}_{CO_2}$ for 33 °C case having a larger value than for 33–38 °C followed by 36 °C case, a trend which was confirmed in plots of the respective quantities (figures not shown). In addition, for each of the T_{cs} cases, we noticed that the Q_{cs} value was only slightly smaller (less than 2%) than the value of Q_{bc} . This implying that the net heat flux (Q_{net}) lost to the air from each bee cover volume is much smaller in value compared to Q_{bc} , i.e., most of the heat generated in the bee cover is transferred to the comb surfaces underneath the bee cover volume.

The difference between the various T_{cs} cases can be seen in plots of integral quantities shown in Fig. 6(a)–(c). Fig. 6(a) shows that Q_{net} value for 33–38 °C is greater than for 36 °C followed by 33 °C in most of the beehive except in the bee cover volume next to the end walls where trend is reversed. The average value of body force (BF_{bc}) shown in Fig. 6(c) for the nonuniform T_{cs} case has a much higher value than for the uniform T_{cs} cases in all bee cover volumes except in the ones near the end walls; the opposite trend

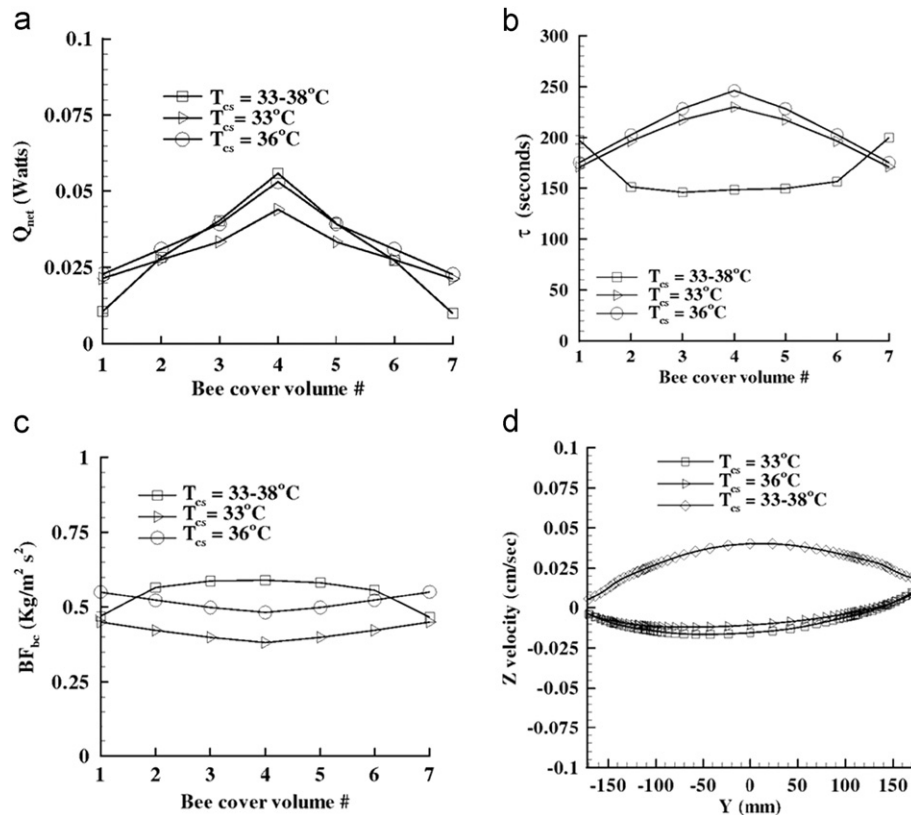


Fig. 6. Plot of different integral quantities in a model beehive with $\beta_{gradient} = 70-30$, $\phi = 0.45$ at $T_{amb} = 20^\circ\text{C}$ for different comb wall temperatures studied in Case A in (a)–(c) along with plot of z velocity along a line through the middle of the central bee cover volume in the beehive for different comb wall temperatures studied in Case A.

is found in plots of pseudo-residence time τ seen in Fig. 6(b) with the nonuniform T_{cs} case showing much lower value than for uniform T_{cs} cases. These trends indicate that the strength of flow through the bee cover volumes for uniform and nonuniform comb wall cases are different. This is confirmed in Fig. 6(d) which shows the z velocity along a horizontal line ($Z = \text{constant}$) running through the middle of the central bee cover volume (bee cover #4) in the beehive for all the three T_{cs} cases. The flow through the bee cover is seen to go upward throughout the central bee cover volume only for nonuniform T_{cs} case, while for both the uniform T_{cs} cases it goes in the opposite direction (top to bottom) for much of the bee cover volume except over a small portion of the bee cover volume located farthest away from the inlet.

The effect of the difference in flow through the bee cover is seen in Fig. 7(a)–(c) which shows the contours of molar concentration of carbon-dioxide (K mol/m^3) on the midplane through the central bee cover volume for different values of T_{cs} . The contours corresponding to higher concentration values in the nonuniform case (Fig. 7(a)) are shifted up and away from the elliptical brood area (Fig. 2(b)) present in the center of the bee cover volume. The average molar concentration of carbon-dioxide shown in Fig. 7(d) shows that $T_{cs} = 33-38^\circ\text{C}$ case has much lower value than value for 33°C and 36°C cases. Thus between the uniform and nonuniform T_{cs} cases, the brood and the worker honeybees in the cluster in the nonuniform T_{cs} case are seen to experience a much lower carbon-dioxide concentration, a condition highly beneficial to the health of the brood and the worker honeybees.

The observed effect of the comb wall temperature is explained as follows. The driving force for the flow at each location inside the bee cover volume (source term in the fluid momentum Eq. (7)) is proportional to difference in density of the air at that location and the reference density (density of air mixture at inlet) $(-\rho - \rho_{ref})g$. This driving force has contributions both from the

heat and mass transfer occurring inside the bee cover volume due to honeybee metabolism, i.e., density is a function of both temperature and species concentration, see (19). Inside each bee cover volume, the heat generated by the honeybees aids this driving force, while the mass transfer which adds denser carbon-dioxide and water vapor to the air mixture has the opposite effect. In the nonuniform T_{cs} case there exists a region of high temperature (38°C) in the center of the comb surface which drops to 33°C over a distance from the edge of this central core region (see Fig. 4). Inside this high temperature core region, the amount of heat and mass of carbon-dioxide and water vapor generated from honey bee metabolism is reduced in value. Among these two effects, namely reduction in heat and mass transfer source terms inside this high temperature core region, it is later which plays the decisive role; this is due to the multiplicative factor in the stoichiometric Eq. (5) for honeybee metabolism, i.e., 6 mol of carbon-dioxide and water vapor produced per mole of honey used up. Thus, the nonuniform comb surface temperature that results from the work of cell heating and surface heating honeybees is seen to enhance the flow through the bee cover volume. However, we notice that although nonuniform T_{cs} drives more flow through the bee cover volume it has a lower value of $\dot{V}_{inflow}$ and η_{CO_2} in comparison to the uniform T_{cs} cases. This implies that all this enhanced flow arising due to honeybee brood warming activities accomplishes is to push the extra carbon-dioxide out of the bee cover volume, but not out of the beehive.

The simulations done in this study were for a steady state case, despite this limitation, it is possible for us to extrapolate from the results presented the net effect we could expect in unsteady case with time varying comb wall temperatures. We speculate that the warm up and cool down phases during brood thermoregulation enhance different gas exchanges needed for the beehive to function efficiently, the first being the gas exchange between the bee

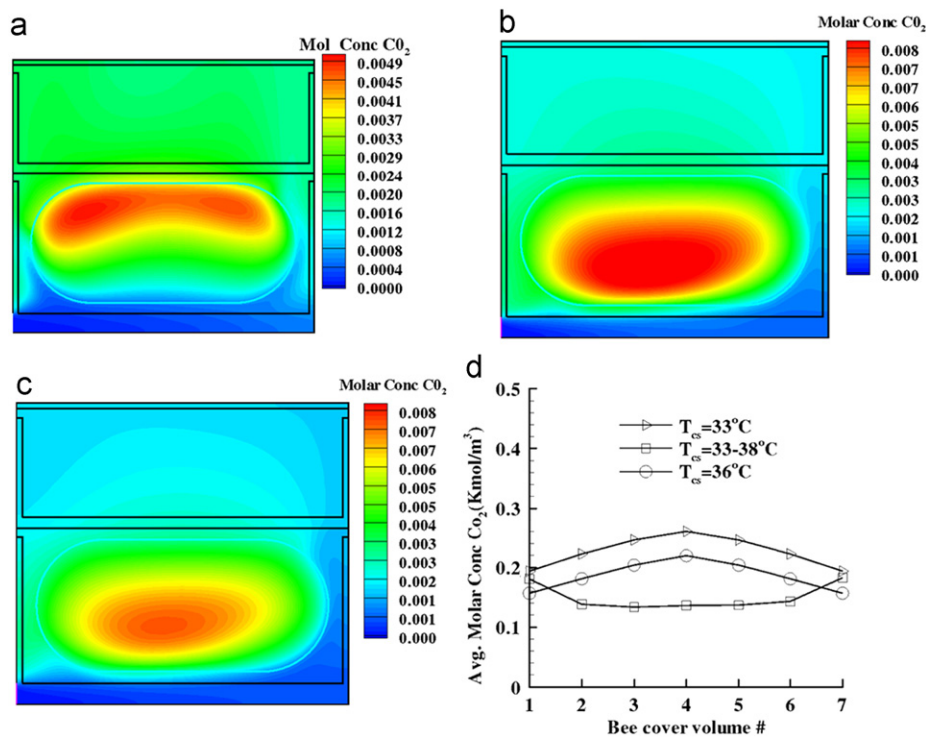


Fig. 7. Contour plot of molar concentration of carbon-dioxide (K mol/m^3) on a YZ plane passing through central bee cover volume (#4 of #7) for different comb wall temperatures studied in Case A where (a) $T_{cs} = 33-38^\circ\text{C}$ (b) $T_{cs} = 33^\circ\text{C}$ and (c) $T_{cs} = 36^\circ\text{C}$ and in (d) plot of average molar concentration of carbon-dioxide in the different bee cover volumes.

cover and the rest of the beehive and the second being the exchange between the beehive and the ambient air. The heating phase which is accompanied by raising comb wall temperature in the central core corresponding to our $33-38^\circ\text{C}$ case drives more flow through the bee cover volumes but at the expense of reduced exchange between the beehive and ambient, while the cooling phase where the comb temperature everywhere decreases and tries to drop below the 33°C drives more flow between the beehive and the ambient. It is to be noted that the nonuniform temperature distribution we have applied on the comb surface assumes that the brood on each comb surface occupies a region which is enclosed by a single curve of some shape (ellipse in our case). However, it is possible for the brood region at different times to consist of separated continuous regions. This would require us to apply a different nonuniform comb surface temperature profile to mimic such a situation. This possibility will be explored in a future study where we take the input data for the cell occupancy obtained from images of comb surfaces.

In summary, the results clearly answer an important question “How do worker honeybees engaged in brood thermoregulation activities which involve increased metabolism drive out the by products – namely carbon-dioxide and water vapor that result from their increased metabolic activity?”. For the rest of the simulations done in case B and C, we used only the nonuniform comb surface temperature instead of the uniform one as it represents a more realistic condition.

5.2. Case study B: effect of changing outside air temperature

The results for case B need to be interpreted carefully, since the model setup does not include explicitly any behavioral or collective colony response that the honeybees might have to changing outside air temperature. This is implied by the model assumptions we use namely that the comb surface temperature profiles applied

and the activity level of the honeybees ($R_{active} = 0.6$) in each bee cover volume does not change as we change T_{amb} .

Fig. 8(a) shows the ventilation inflow rate at different values of outside air temperature (T_{amb}) in a model beehive with $\beta_{gradient} = 70-30$ ($70-50$ case not shown reflects similar trend) for different values of the bee cover porosity (ϕ). Ventilation flow rate decreases with increasing T_{amb} in all cases, but the rate of decrease varies. For $\phi = 0.4$, where conduction inside the bee cover is expected to dominate, the rate of decrease as T_{amb} increases is constant. For $\phi = 0.45$ and 0.5 , the rate of decrease varies as the outside temperature increases, i.e., the slope changes. Fig. 8(b) shows the same data plotted to show the effect of varying porosity at a given value of T_{amb} ($70-50$ case not shown reflects similar trend).

The change of ϕ in a bee cover volume can be accomplished in two ways, one by changing the volume occupied by the bee cover via expansion or contraction while keeping the number of honeybees in it constant, or by keeping bee cover volume constant and varying the number of honeybees in it. For some simulations done in case C it was done in the former way, while for the current case (case B) it was accomplished the latter way. In this setup, the change in ϕ has two important effects on the flow, one through changing the amount of heat and mass generated due to a change in the number of honeybees and second through change in the resistance encountered by flow in the porous bee cover volume. The net effect of changing porosity at a given ambient temperature depends on how these two effects balance each other, which explains the different trends we observe in Fig. 8(b). For example, consider the effect of increasing ϕ from 0.4 to 0.5 at $T_{amb} = 17.5^\circ\text{C}$ in Fig. 8(b). When we increase ϕ from 0.4 to 0.45 , it reduces the number of honeybees and thereby the heat and mass generated that drives the natural convection flow, but this reduction is compensated by the fact that the flow experiences less resistance, thus ensuring that ventilation flow rate does remain more or less constant. In contrast, when we

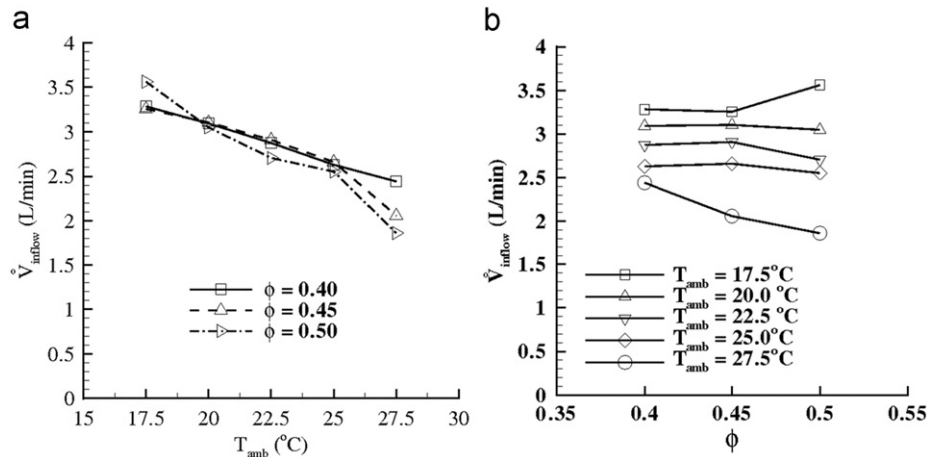


Fig. 8. Plots of ventilation flow rate (L/min) at different values of T_{amb} and at different values of ϕ in a model beehive with $\beta_{gradient} = 70-30$.

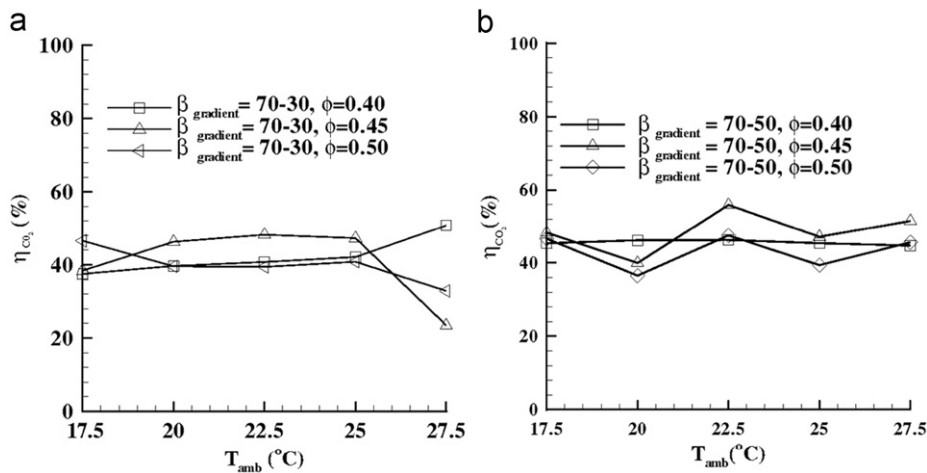


Fig. 9. Plot of carbon-dioxide clearance efficiency at different values of T_{amb} in a model beehive with $\beta_{gradient} = 70-30$ in (a) and $\beta_{gradient} = 70-50$ in (b).

increased porosity further from 0.45 to 0.50, the effect of further lowering the flow resistance dominates and the ventilation flow rate increases. Fig. 9(a) shows the plot of carbon-dioxide clearance efficiency in model beehives with $\beta_{gradient} = 70-30$ as T_{amb} is varied. The carbon-dioxide clearance efficiency is seen to change little as we vary T_{amb} from 17.5 °C to 25 °C and it experiences an increase for $\phi = 0.4$ and a decrease for $\phi = 0.45$ and 0.5 as T_{amb} is increased further to 27.5 °C (70–50 case not shown reflects similar trend).

The functional form – linear with negative slope – assumed for the source terms in the governing Eqs. (14) and (17) would lead us to expect that the amount of heat and mass generated by the honeybees would vary proportionally as the outside air temperature T_{amb} changes. However, we observed (figure not shown) that both the heat generated (Q_{bc}) and mass of carbon-dioxide generated per second ($\dot{M}_{CO_2}$) in the different bee cover volumes remained the same as we varied the ambient air temperature. This implying that the average air temperature inside each bee cover volume does not change much as we vary T_{amb} , indicating that it depends more on the comb wall temperature which we keep constant in this case as we vary T_{amb} than on the ambient air temperature. In addition, it means that the ambient air from the outside at lower temperature is warmed up before entering the bee cover volume. We believe that this preheating is achieved by the routing of the inlet air which will be explained in Section 5.4 where we describe the structure of the 3-D flow inside the beehive.

The observed change in ventilation flow rate is explained by looking at the net heat flux (Q_{net}) from each bee cover and the molar concentration of species inside the bee cover volumes both of which affect the driving body force term in fluid governing equations. Fig. 9(b) shows the net heat flux lost to air from each bee cover volume for different values of T_{amb} . Q_{net} decreases as we increase T_{amb} , indicating that Q_{cs} increases. This implying that at higher ambient air temperatures if same comb surface temperature is maintained as we have assumed, heat transferred to comb surface or brood from honeybees inside the cluster increases. This from the point of view of the brood is not healthy, implying that in such a case the cell and wall heating honeybees engaged in brood thermoregulation would adjust their work and their by prevent the comb wall temperature from raising. In the context of our model, though not considered in the current study, this would imply changing R_{active} as T_{amb} increases. In addition, the net heat flux lost to air shown in Fig. 9(b) at low ambient air temperature shows a strong variation across the beehive as we move away from the central bee cover volume towards the one near the end wall, which can be correlated to the 3-D structure of the flow inside the beehive.

In comparison to the change in Q_{net} , the change in concentration of carbon-dioxide is more pronounced as T_{amb} is increased. In an average, except for $\phi = 0.4$ in which case the average carbon-dioxide concentration has a higher value which remains constant as T_{amb} is varied, the average concentration in the bee cover

volumes increases as T_{amb} is increased (figure not shown). This coupled with the fact highlighted earlier that rate of production of carbon-dioxide remains constant as T_{amb} is varied, indicates that at low ambient temperatures bulk of carbon-dioxide produced is removed by the flow through the bee cover volumes. The accumulation of carbon-dioxide inside each bee cover volume as we increase T_{amb} reduces the driving body force as seen in Fig. 10(a) which reduces the flow through the bee cover volume. It is also noticeable from Fig. 10(a) that the rate at which the average body force drops is different for the central (bee cover #4) and near end wall (bee cover #7) bee cover volume as well as on ϕ .

Fig. 10(b) shows the plots of z velocity along a line through the middle of the central bee cover volume (#4 of #7) at different value of T_{amb} . We notice that the structure of the flow through the bee cover changes as we increase T_{amb} , with the flow rising upwards throughout the bee cover volume cross-section at lower value of T_{amb} , while at higher value of T_{amb} , the flow is seen to oriented from top to bottom except over a small segment located near the end wall farthest from the inlet. Fig. 10(b) shows the z -velocity along the entire line through middle of bee cover volume extending from front wall of the beehive to back wall. It shows at low ambient temperatures, a strong boundary layer type flow localized at the bee-cover (porous)–free fluid interface rising all around the bee cover volume while at intermediate and higher ambient temperature it shows a flow going downwards from top to bottom. In addition, we notice that the flow through the honeybee cluster (porous in our model) seen in Fig. 10(b) is several order of magnitude smaller than the flow around the cluster seen in Fig. 10(c).

Fig. 10(d) shows the plot of average molar carbon-dioxide concentration in central (bee cover #4) and near end wall (bee cover #7) at different values of T_{amb} . The concentration is seen to increase at we increase the temperature from 25 °C to 27.5 °C for $\phi = 0.50$, while it increases gradually over the entire range of temperature for $\phi = 0.45$ while it remains constant and high for $\phi = 0.40$. The carbon-dioxide concentration indicative of the changing flow through the bee cover as we increase T_{amb} .

5.3. Case study C: effect of varying porosity inside the beehive

In this case, we did a total of seven runs all at $T_{amb} = 20$ °C in a model beehive with $\beta_{gradient} = 70-30$. Of these seven runs, first three corresponded to case where porosity was held uniform across bee cover volumes inside the beehive and set to $\phi = 0.40, 0.45, 0.50$ respectively, for runs 1, 2 and 3. The 4th and 5th run corresponded to case where keeping the volumes of the bee cover fixed, the porosity in the different bee cover volumes away from central bee cover volume was increased for run 4 and decreased for run 5. For runs 6 and 7, the porosity in all bee covers in the model beehive with $\beta_{gradient} = 70-30$ was initially set to 0.40 in case of 6 and 0.50 in case of 7, and the bee cover volumes were expanded for run 6 and contracted for run 7 to achieve the same porosity variation as in run 5 and 6. The values of the porosity set in each bee cover volume for each of the seven simulations is given in a table in the supporting material. In each of the runs (from #4 to #7) where we assumed porosity variation,

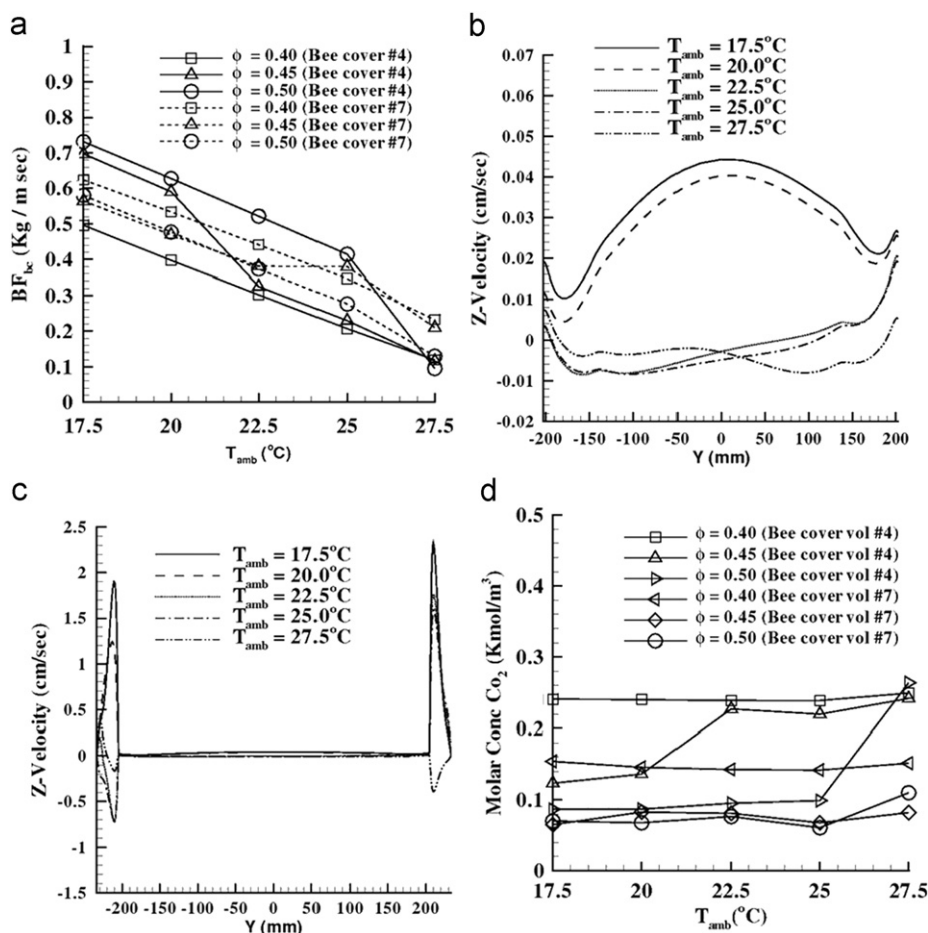


Fig. 10. Plots of (a) pseudo-residence time (τ) in all bee cover volumes at different values of T_{amb} studied in Case B (b) z velocity (cm/s) along a mid line through central bee cover volume (#4) where only the portion of the line inside the bee cover is shown and (c) z -velocity (cm/s) along entire mid line at different T_{amb} for simulations in Case B (d) average molar concentration of carbon-dioxide in central and end wall bee cover volume at different T_{amb} .

we assumed that its variation about the middle bee cover volume is always symmetric.

The results not shown here but in supporting material can be summarized as follows (a) The parameters like ventilation flow rate and carbon-dioxide efficiency did not show any dramatic change when the number of honeybees inside the beehive was changed by varying ϕ while keeping bee cover volumes fixed. In addition, comparing run 6 with run 1 (uniform porosity in beehive case), which have the same number of honeybees, we noticed that the expansion of the bee cover volume to achieve desired porosity variation has little effect on the ventilation inflow rate and carbon-dioxide clearance efficiency. Similarly, comparing the values for run 7 with run 3, which have the same number of honeybees, we noticed that contraction reduces the flow through the beehive as expected; causing a reduction in the ventilation flow rate and carbon-dioxide clearance efficiency. In addition, comparison of the computed integral quantities in each of the bee cover volumes in the seven runs, indicates that the quantities in each of bee cover volumes are affected only by the porosity value set in the bee cover and very little by the changing conditions (i.e., porosity) in the bee cover volumes next to it.

The implications of this to the honeybees is important, it implies that the worker honeybees in each bee space via setting the value of porosity and the comb surface temperature have some control over the vital conditions like average carbon-dioxide concentration in their cluster and they are not influenced by what is happening or conditions present in the honeybee clusters present in the adjacent bee spaces. This aspect relates to the stability of the flow inside the beehive and requires much closer attention than what we have devoted in this study, which should be explored as a part of the future work.

5.4. Structure of the flow

The flow inside a beehive is expected to be three-dimensional and complex. To understand its features, conventional flow visualization techniques like cut planes, contour plots, path lines were employed. Of the three, we used pathlines extensively to look closely at the structure of the flow. A path line is a plot of the trajectory that an individual (mass less) fluid particle follows as it is gets convected by the flow field inside the fluid domain. A path line is initialized by specifying an initial starting location in the fluid domain from where the fluid particle is released. We have initiated path lines starting from points on the inlet face of the beehive as well as from points inside the different bee cover volumes. In addition to functioning as a tool to visualize the flow

field, path lines can also be colored to indicate the value of scalar variables like concentration or temperature along their path. A path line is constructed by integrating in time the initial value problem (IVP):

$$\frac{d\vec{X}}{dt} = \vec{U}(x,y,z,t), \quad \vec{X}(t=0) = \vec{X}_0 \quad (34)$$

where $\vec{X}(t)$ is the position vector giving the coordinates of the fluid particle whose trajectory is the path line, $\vec{X}_0$ the initial starting location and $\vec{U}$ is the spatially varying velocity field in the fluid domain. A detailed discussion of the features that can be used with path line tool available in the Fluent® is available in the user manual (ANSYS Inc., 2006).

In the rest of this section, we will use the simulation results from a model beehive with $\beta_{\text{gradient}} = 70-30$, with $\phi = 0.45$, $T_{\text{cs}} = 33-38^\circ\text{C}$ and $T_{\text{amb}} = 20^\circ\text{C}$ to illustrate the structure of the flow. A brief review of the salient features of the flow along with supporting figures will be provided in the section. Animations using pathlines arising from flow visualizations along with other supporting figures to highlight the flow features are provided as supplementary material with this article. A complete listing of the content provided as supporting material to this paper is provided in Appendix.

Following observations can be made about the structure of the flow inside the beehive from our detailed analysis.

- The flow enters the beehive through the bottom $\frac{2}{3}$ rd (maximum velocity of around 1 cm/s) and exits it through the top $\frac{1}{3}$ rd of the inlet cross-section (maximum velocity of around 3 cm/s) (Fig. 11). Fig. 11(c) shows that the flow entering the beehive is completely normal to the inlet plane, with both in plane velocities – namely x and z velocities being zero, while the flow exiting the beehive does have non-zero in plane velocities (see Fig. 11(c)) indicating the presence of vortices. The vortices are also clearly seen in Fig. 12(b) which shows path line of particles introduced at different locations along the inlet.
- Fig. 12(a) shows path lines introduced at different locations on the inlet face in front of bee cover volume #4. The path lines shown in Fig. 12(a) are the trajectories at the end of integrating path line IVP (Eq. (34)) for 250 time steps with a time step $\Delta t = 0.1$ s. They are colored based on temperature of the air at each location along their path. The pathlines shown in Fig. 12(a) shows that air entering the beehive at the inlet is transported all the way towards the other end wall located opposite to the inlet face and then transported back in the opposite direction towards the inlet during which time they

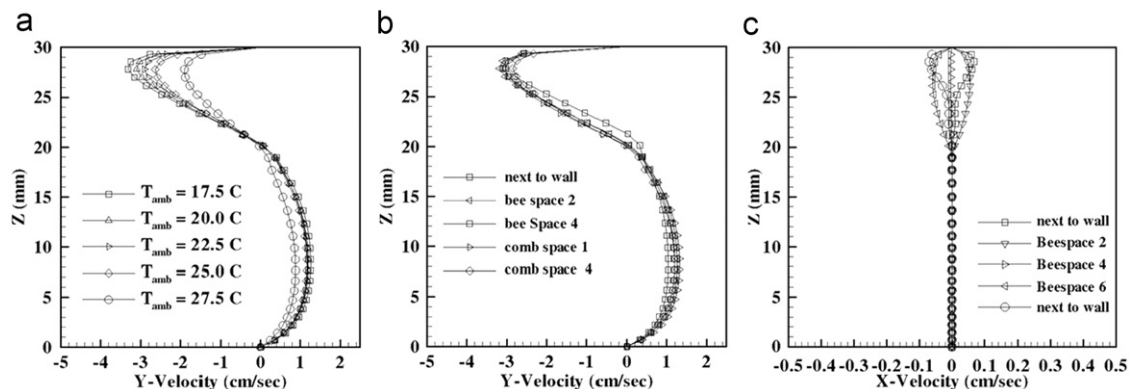


Fig. 11. Plot of velocities along vertical lines in the inlet plane to the beehive where (b) and (c) show x and y velocities (see Fig. 3 for orientation of coordinate system) in front of different bee spaces and (a) shows y velocity in front of the central bee space (front of bee cover volume #4) at different T_{amb} studied in Case B.

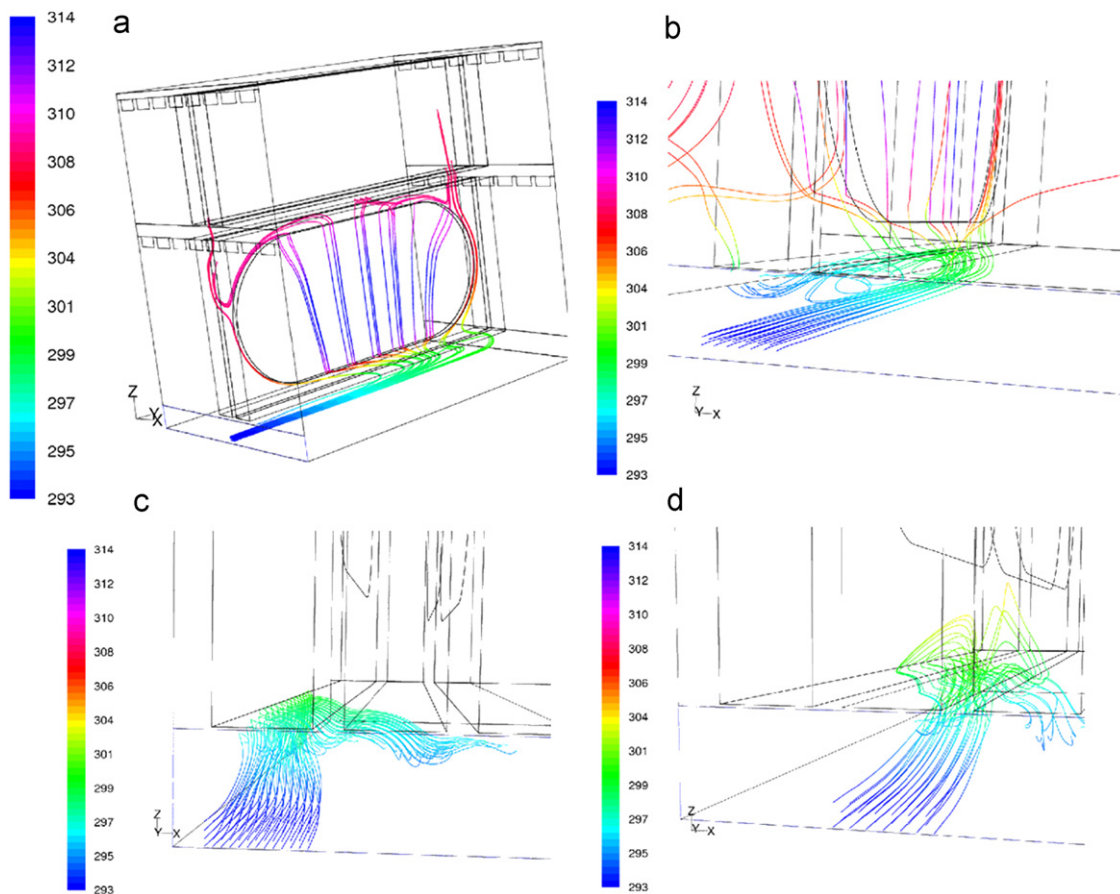


Fig. 12. Plot of path lines colored by temperature (in Kelvin) introduced at different locations in the inlet plane in a beehive with $\beta_{\text{gradient}} = 70-30$ at $T_{\text{amb}} = 20^\circ\text{C}$.

- enter into the bee space and then into the bee cover volume. In addition, we notice that as we follow the path of the fluid particles, the color of the path lines change indicating that air entering from the inlet at low temperature is warmed up rapidly before it enters into the bee space. In Fig. 12(b), we see path lines entering the beehive from locations in inlet positioned in front of one of the frames. In the figure, we notice clearly that the path line shows a distinct curliness when the flow is returning back towards the inlet face from the other wall. This waviness results from the presence of vortices located underneath the frames. This routing of the flow which brings into contact cold denser air entering the beehive and the warm lighter air leaving out of the beehive coupled with the mixing provided by the vortices present beneath the frames gives a heating effect similar to that in a counter current heat exchanger. This counter-current flow routing of the inlet and exit air ensures that some portion of the heat lost from the bee cover volumes is recovered and used to preheat the incoming colder ambient air.
- The presence of the end walls along the span (next to the frame #1 and frame #8 in a 8 frame beehive) and the no-slip boundary condition imposed by it on the flow sets up an adverse span wise pressure gradient ($\partial p/\partial x$) in the air space below the brood chamber. This adverse pressure gradient affects the flow entering the beehive in the locations near the vicinity of the end walls. Fig. 12(c) and (d) shows the path lines introduced at different locations in the inlet in front of different frames near the span wise (along X direction with respect to coordinate system in the figure) end walls. The orientation of the path lines displays a distinct slant towards

the span-wise end wall of the beehive which is the result of this pressure gradient.

- The bee space or spacing between comb faces on adjacent frames is less than $\frac{1}{3}$ rd the thickness of the frames, which ensures that only a fraction of the flow entering the beehive reaches up into the bee space while the rest of the flow exits the beehive without ever entering the bee space. This feature which we term “by-pass” is characteristic of the non-displacement type ventilation prevalent in enclosures with only one opening. The portion of the flow which does not enter the bee space, however, contributes to removing the heat and species produced in the bee cover volumes, which possibly contributes to the more than 50% carbon-dioxide removal efficiency we notice in Fig. 9.
- The flow that rises up into the bee space encounters the porous bee cover. A part of the flow goes through the bee cover volume, the extent of which depends on the porosity of the bee cover volume. The remaining part flows around the bee cover volume like it would around a solid bluff body. The porosity of the bee cover ϕ determines both the resistance offered to the flow as well as the amount of heat and mass generated in each bee cover volume.
- Each bee space is a 3-D air space resembling a rectangular enclosure with large aspect ratio (length and width $\gg$ thickness) which ensures that the flow in it is essentially two dimensional. Fig. 13 shows the plot of path lines released from inside different bee covers, which shows that the path lines exiting the different bee covers separate out to form two large recirculating vortices much like a wake behind a bluff body. These vortices occupy much of the bee space in the honey super and they trap much of the carbon-dioxide and water

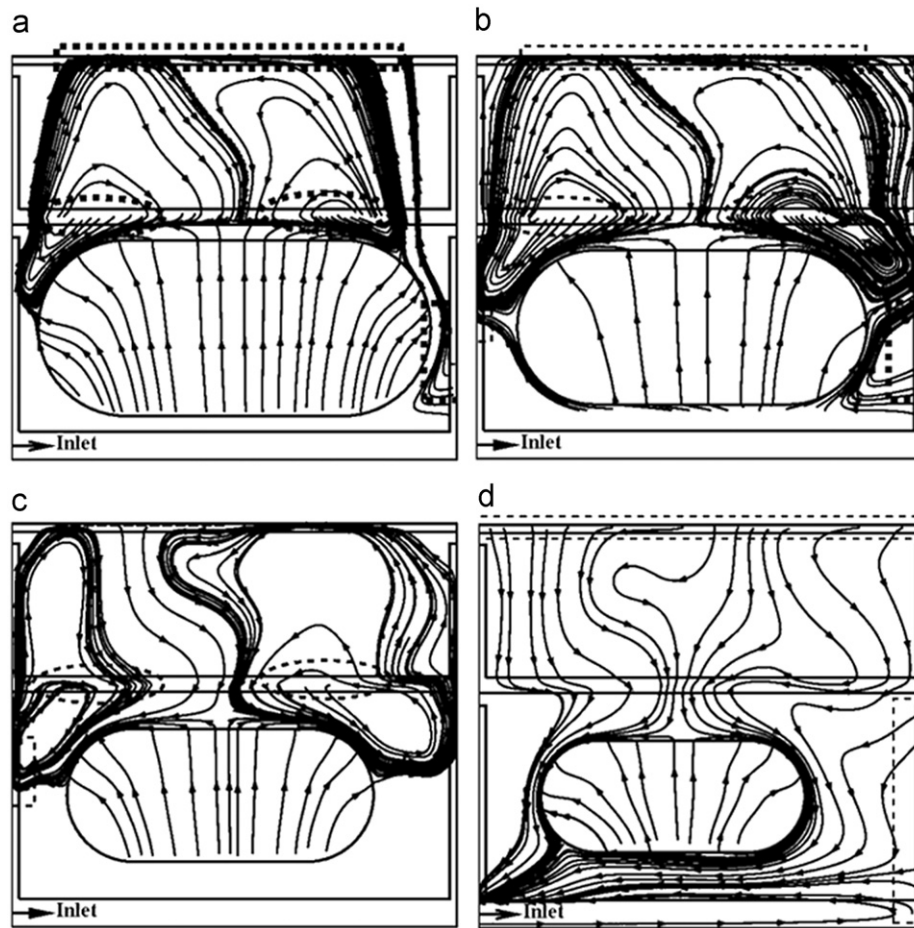


Fig. 13. Plot of path lines introduced at different locations inside the bee cover volumes in one half of a beehive with $\beta_{\text{gradient}} = 70\text{--}30$ at $T_{\text{amb}} = 20^\circ\text{C}$. The area marked with dotted line indicates regions where vortices that occupy much of the bee space in the honey super interact with the vortices in the adjacent bee spaces.

vapor which are produced in the bee cover volumes as a result of honeybee metabolism and transported away from there by the flow through the bee cover. The recirculating wake like vortices above the bee covers in the space between the frames in the honey super are the influence of mass transfer. They are not observed if the problem is modeled as a heat transfer alone problem, i.e., if mass transfer resulting from honeybee metabolism is neglected.

- The flow in the first and last bee cover volume which are next to end walls of the beehive are predominantly from top to bottom outside the bee cover volume as seen in Fig. 13(d) where in addition path lines originating from inside the bee cover, path lines are started from the air space between the honey super frames and the top of the beehive. The wake like vortices in the downstream of the bee cover volumes are absent in the first and last bee spaces which support a bee cover volume (bee cover #1 and #7).
- The flows in adjacent bee spaces interact or mix with each other via the middle air space which separates the brood chamber and the honey super as well as in the space between the frames and the outside walls of the beehive. The dotted box in Fig. 13(a)–(d) shows regions where this happens.
- An animated file (movie file in windows WMV format) of path lines for $T_{\text{amb}} = 17.5^\circ\text{C}$ and one for $T_{\text{amb}} = 27.5^\circ\text{C}$ are made available as supplementary material to this paper. In the animation, for the purpose of visual clarity, each path line is shown in a different color. We observe the mixing between the wake vortices in adjacent bee spaces. Also clearly visible in the animation would be path lines which enter and exit out of

the beehive without entering into any of the bee spaces supporting the bee cover volumes.

- At a higher T_{amb} , when the ventilation flow rate decreases, the structure of the flow also changes. In contrast to observations at $T_{\text{amb}} \leq 25^\circ\text{C}$, at $T_{\text{amb}} = 27.5^\circ\text{C}$ the flow does not penetrate all the way to the other end of beehive boundary opposite of the inlet, but reaches only midway. At lower T_{amb} , the flow in the bee space rises all round the bee cover volume as seen in Fig. 12(a), while at $T_{\text{amb}} = 27.5^\circ\text{C}$ the flow from pathlines shown in Fig. 14 is seen to rise upwards in the upstream or front side of the bee cover volume closest to inlet while it is directed downwards along the side of the bee cover farthest from the inlet. The flow that arrives downward on the backside farthest from the inlet is seen to form vortices in the bottom space below the frames in the brood chamber. These vortices as seen in Fig. 14 have an orientation slanted towards the bottom corners of the beehive.
- Both the porosity of the bee cover, ϕ and its variation across bee covers across the bee hive β_{gradient} have an effect on the mixing pattern between flows in adjacent bee spaces (not shown in any figure). Larger β_{gradient} enhances mixing. The mixing pattern between the flow in different bee spaces changes as ϕ changes, with increasing porosity seen to enhance mixing.

6. Summary and conclusions

Ensuring sufficient ventilation to a beehive is recognized universally by practicing beekeepers as an essential prerequisite

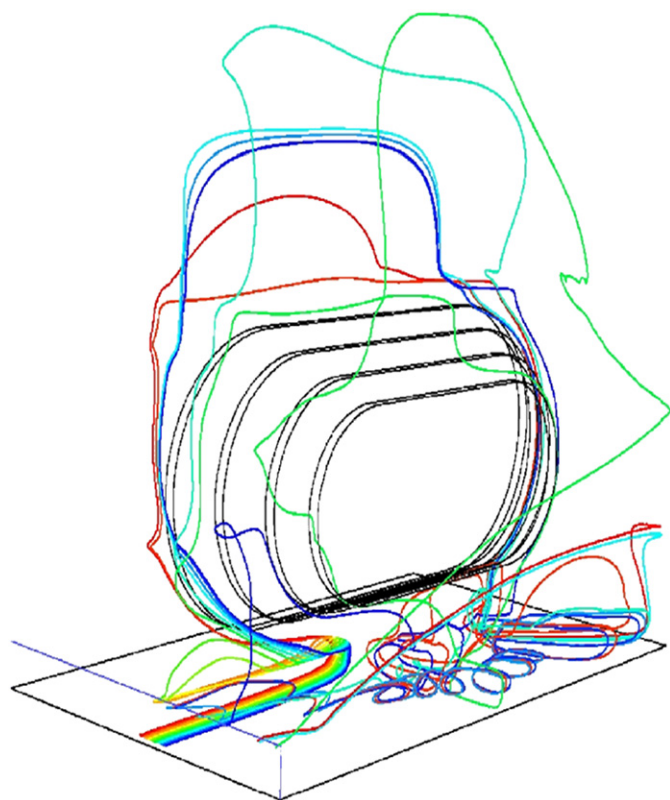


Fig. 14. Plot of path lines introduced in front of frame #5 in a model beehive with $\beta_{\text{gradient}} = 70\text{--}30$ at $T_{\text{amb}} = 27.5^\circ\text{C}$. Each path line is colored differently for visual perception. For purpose of visual clarity, the frames and the walls of the beehive in brood chamber and honey super have been made transparent and only the bee cover volumes in one half of the beehive has been shown.

for sustaining a healthy colony inside it. Ventilation of a beehive consists of two interconnected processes happening simultaneously, the first being the intra-beehive exchange between the honeybee and the air inside the beehive and the second being the inter-beehive exchange between the beehive and the ambient air. Of the two, only one aspect of inter-beehive ventilation has received maximum attention in the literature namely the fanning response initiated during warm summer days when honeybees sit at the entrance of the beehive and fan their wings to force warm and stale air out of the beehive and draw fresh air into the beehive (Seeley, 1974; Southwick and Moritz, 1987). Aside from the discussions on fanning response which is triggered only under extreme conditions (high temperature or high carbon-dioxide concentration inside the beehive), very little quantitative and qualitative knowledge is available about how ventilation of a beehive works under moderate conditions like those that prevail during mild spring and summer days. This knowledge gap prompted us to undertake this study aimed at understanding the flow inside the beehive.

We chose to setup and solve the fluid flow model numerically using FLUENT®, a commercially available Computational Fluid Dynamics (CFD) solver routinely used by engineers to understand ventilation of different enclosures like operating theaters in hospitals, green houses, etc. Having chosen an engineering approach, at the onset we realized that the scale and scope of our model (beehive with a brood present in it during the summer) was much bigger and different than anything modeled before in the context of honeybees; the earlier models being limited to modeling winter thermoregulation in a honeybee cluster present inside a beehive with no brood or a honeybee swarm hanging outside on a tree branch. With this

backdrop, we set out to collect information about how the different contents (honeybees, brood, pollen, empty cells, honey) are distributed inside the beehive by conducting our own regular photographic inspection of beehives held at the Honey Bee Research Center at University of Guelph as well as enlisting the help of local beekeepers through a survey mailed to them. With these efforts, we arrived at a small set of parameters with which we could parameterize the distribution of contents inside the beehive, assigned nominal values to these parameters to use in our study and finally constructed a 3-D geometric model of a beehive inside which we simulated the fluid flow.

In our formulation, we avoided treating the several thousand honeybees inside the beehive individually but choose instead to model each honeybee cluster inside the beehive as a porous medium. Within this porous medium modeling framework, we accounted for the different heat and mass transfer interactions between the honeybees and air arising due to honeybee metabolism using source terms in the governing equations. To make this model tractable and computationally feasible, we invoked several assumptions and model simplifications (see Section 3.2), some of them like constant porosity in each honeybee cluster necessitated due to lack of sufficient data to fix its variation. For our first study, we limited the ambient air temperature to be under 30°C and in this temperature range solved for the flow inside the beehive after applying a carefully constructed temperature profile on the comb surfaces to mimic brood thermoregulation that is active in this temperature range, with this completing our objectives (a)–(d) listed in Section 1.5.

The new understanding we have gained from our current study about how ventilation works at lower ambient temperatures when fanning is not active (objective (e) listed in Section 1.5) can be summarized as follows: (a) Mass transfer associated with honeybee metabolism plays a significant role in directing the flow through and around the honeybee clusters in the beehive and accumulation of species like carbon-dioxide and water vapor inside the honeybee clusters reduces the flow through them and this affects the flow in rest of the beehive. (b) The spatially nonuniform temperature conditions that prevail on the comb surfaces present underneath the different honeybee clusters inside the beehive drives more flow through the honeybee cluster. This enhanced flow removes much of the carbon-dioxide and water vapor produced inside the honeybee cluster, thereby preventing the exposure of the brood on the comb surface to higher concentration of carbon-dioxide. (c) As observed by practising beekeepers, at higher ambient air temperature close to 30°C the strength of the natural convective flow into and out of the beehive decreases and under these conditions most of the carbon-dioxide produced inside the beehive remains inside the beehive. In addition, we observed that at these high ambient air temperatures, only the front part of the beehive was served with fresh air entering from the inlet, leaving large portions of the beehive stagnant with very weak flow.

From the fluid mechanics point of view, extensive visualization of flow inside the beehive conducted indicates that (a) the flow is 3-D with only a fraction of the flow entering the beehive through the inlet entering the bee spaces; (b) the routing of the flow at lower T_{amb} is seen to heat the air entering the beehive before it enters into the bee space. This heating up is enhanced by the vortices and counter current flow setup present in the space between the frames in brood chamber and the bottom board; (c) the flow around the bee covers is seen to separate out to form wake like recirculating vortices which occupy bulk of the bee space in the honey super. The vortices in adjacent bee spaces were found to interact with each other primarily along the mid volume separating the brood chamber and the honey super.

For the simulations done in the study, when we change the ambient air temperature or the porosity in the different honeybee clusters we have neglected any colony wise response honeybees might have to changing conditions inside the beehive by assuming that the temperature we applied on the comb surface which has the brood is kept constant and that the activity level of honeybees present in the different clusters is held constant ($R_{active} = 0.6$). With these model constraints in place, the only true indicator we have to access the stress experienced by the honeybees is the concentration of carbon-dioxide experienced by the honeybees. At low T_{amb} for moderate values of honeybee cluster porosity we notice that concentration of species inside the honeybee clusters is low, i.e., fraction of carbon-dioxide produced in the honeybee cluster that stays inside the cluster is low. The low concentration of carbon-dioxide resulting from enhanced flow inside the honeybee cluster implies that the brood covered by the honeybee cluster is kept away from exposure to high carbon-dioxide concentration, which is a good effect of having sufficient ventilation in the presence of brood thermoregulation. However, because of our model constraints, we have to be careful not to draw the wrong conclusions from the results seen in the plots as we increase the ambient temperature. For example, Fig. 10(d) shows that the average concentration of carbon-dioxide experienced by the honeybees in central and end wall honeybee clusters increases when ambient temperature increases, possibly suggesting increasing stress on the honeybees. However, we believe this would be corrected by the honeybees by reducing their activity level as well as by changing the comb surface temperature by reducing the work of the cell heating honeybees, a possibility which we did not allow for in the running of the model but can be easily incorporated into the model.

From the point of view of pest management which is related to taking care of the health of the colony, results from our study in the ambient air temperature range $17.5^{\circ}\text{C} < T_{amb} < 27.5^{\circ}\text{C}$ indicate that in this range the ventilation flow rate is moderate, residence time (RT) of any particle entering the beehive is low, and air inside the beehive outside the honeybee clusters is well mixed. The improved ventilation at low ambient temperatures has two implications in the case of a beehive infested with pathogens like Varroa mites (Eberl et al., 2010), first a strong flow inside the beehive accompanied by low RT would increase the likelihood of the mites shaken off from honeybees to be transported out of the beehive by the flow before they can latch on to and infect another healthy honeybee and second, any chemical treatment applied to the beehive in the form of sprays or spores to treat an infested beehive would be transported by strong flow inside the beehive and distributed evenly to the different affected areas inside the beehive.

The basic modeling frame work developed in this work can be easily extended and applied to find answers to questions of interest to beekeepers, for example, whether a particular hive modification like adding a hole enhances the flow inside the beehives. Just recently, we completed another study (Thompson, 2010) where we used the model developed in this study to examine how changes in the bottom board shape affects ventilation inside the beehive. The geometric model of the beehive with its contents provides ample scope for improvement with availability of new data. In the model side, couple of the extensions we are working to add to our current model are to account for the mass transfer contributions resulting from curing of honey in the honey super as well as to try include honeybee colony wise responses like contraction/expansion of clusters in response to conditions inside the cluster. Over all, we believe that our model and results presented here have brought to light hitherto unexplored flow conditions inside a beehive.

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Appendix A. Summary of Supporting material

The supporting materials provided along with this paper are as follows

- Supporting-Material-Effect-of-Brood-Thermoregulation.pdf: a pdf file named which contains figures and tables.
- Six WMV files: Tamb-17-5C-part1.wmv, Tamb-17-5C-part2.wmv, Tamb-17-5C-part3.wmv and Tamb-27-5C-part1.wmv, Tamb-27-5C-part2.wmv and Tamb-27-5C-part3.wmv in which we show the animation of path lines introduced into the beehive from the inlet at $T_{amb} = 17.5^{\circ}\text{C}$ and at $T_{amb} = 27.5^{\circ}\text{C}$ respectively. The three parts of the file correspond to one single animation file split into three parts because of upload size limitations and should be played back to back.

In the rest of this appendix, a brief description is provided to explain figures you will see in pdf file relevant to different sections of the paper. The figure numbers we refer to in the rest of the appendix refer to figures in the pdf and not to the main paper.

A.1. Figures related to Section 2.3

- Fig. 1 shows a copy of the two page survey we circulated among the local bee keepers to get their feed back regarding the shape of the honeybee cluster and brood inside the beehive.
- Fig. 2 shows the pictures of brood area on a comb surface at different times in the season, early spring and start of summer.
- Fig. 3 shows the pictures of brood area on the two comb surfaces that make the central bee space inside a beehive. The purpose of this figure is to illustrate that the brood on adjacent comb surfaces that make up the bee space is almost coincident like we have assumed in our model.
- Fig. 4 shows the pictures of comb surfaces in one half of a beehive making up the different bee spaces. It is clearly seen that (a) the comb surface next to the wall has no brood and (b) that the size of the capped brood area increases from the surface near to the end wall to the comb surface in the center of the beehive.

A.2. Figures related to Section 4.2

- Fig. 5 shows the projection of the computational grid used in this study on a YZ cut plane passing through the middle of the beehive through the central bee cover volume (bee cover

volume #4). Note the clustering of grid near the interface between the porous bee cover and the free air in the beehive.

- Fig. 6 shows the projection of the computational grid used in this study on a XZ cut plane through the middle of the beehive.

A.3. Figures related to role of mass transfer

The set of Figs. 7–9 compare the results of two sets of simulations one in which we take into account the effect of mass transfer that takes place during honeybee metabolism on density of air via equation of state (Eq. (19)) and the second set in which we neglect the effect of this mass transfer on density of air (i.e., equation of state for air depends on temperature alone). In the second case, when we neglect effect of mass transfer on density, we solve a scalar transport equation for the different species in the air mixture namely carbon-dioxide, water vapor and oxygen. Though in hindsight including the effect of mass transfer on density might seem obvious, it is to be borne in mind that almost all the previous models related to honeybees deal only with heat transfer aspect of honeybee metabolism. In that context, it was important for us to establish early on in our work, how much effect mass transfer has on the flow.

- Fig. 7 show the ventilation flow rate for the two cases—heat transfer happening during honeybee metabolism alone drives the flow and both heat and mass transfer happening during honeybee metabolism drives the flow inside the beehive.
- Fig. 8 shows the contour plot of carbon-dioxide molar concentration in the central and end wall bee cover volumes for these two cases—heat transfer alone drives the flow and heat and mass transfer drives the flow. We clearly notice the effects of not taking into account mass transfer related to honeybee metabolism.
- Fig. 9 shows the vector plot on a YZ plane through the middle of the central bee cover volume for the two cases—heat transfer alone drives the flow and heat and mass transfer drives the flow. We clearly see looking at the region in the honey super the difference, in heat and mass transfer case, we see the presence of vortices occupying much of honey super and not in case of heat transfer alone.

A.4. Figures related to Case C

- Table 1 shows the value of ϕ in each of the seven bee cover volumes for different simulations done in Case C. For # 6 and #7 the change in porosity was achieved by methods described in paper.
- Fig. 10 shows the shape of the bee cover volumes before and after expansion for run #6 and before and after contraction for run #7 in Case C. The dark line shows bee cover volume location before and lighter line after expansion for run #6 and contraction for run #7.
- Table 2 shows ventilation inflow rate ($\dot{V}_{inflow}$), total carbon-dioxide generated per second ($\sum \dot{M}_{CO_2}^i$) inside the beehive, mass flux of carbon-dioxide out of the beehive ($\dot{M}_{CO_2}^{out}$) and carbon-dioxide clearance efficiency (η_{CO_2}) for the different runs in Case C.
- Table 3 shows mass of carbon-dioxide generated per second ($\dot{M}_{CO_2}$) and pseudo-residence time (τ) in the different bee cover volumes present in one half of the beehive for different runs done in Case C.
- Table 4 shows average molar concentration of carbon-dioxide and average body force in the different bee cover volumes present in one half of the beehive for the different runs done in Case C.

A.5. Figures related to Section 5.4 (structure of flow)

- Fig. 11 shows in a schematic the location of different lines (L1–L5) in YZ plane aligned with different bee spaces along which different velocities are shown in subsequent Figs. 12–16.
- Fig. 12 shows lot of velocities along lines aligned with different bee spaces at $T_{amb} = 20^\circ\text{C}$ for beehive with $\beta_{gradient} = 70-50$ (a) z velocity at top of the brood chamber (L1), (b) z velocity at the entrance to the honey super (L3), (c) x velocity in the middle space between honey super and brood chamber (L2), (d) x velocity in air space between the top wall of the beehive and honey super (L5). We can clearly see comparing the reduction in z velocity seen from (a) to (b) that some of the flow raising out of a bee space is mixing into the adjacent bee space through the mid volume space between the honey super and the brood chamber.
- Fig. 13 shows plot of velocities along same lines as done one in Fig. 12 for run #1 done in Case C ($\beta_{gradient} = 70-30$, uniform porosity $\phi = 0.40$).
- Fig. 14 shows plot of velocities along same lines as done one in Fig. 12 for run #2 done in Case C ($\beta_{gradient} = 70-30$, uniform porosity $\phi = 0.45$).
- Fig. 15 shows plot of velocities along same lines as done one in Fig. 12 for run #3 done in Case C ($\beta_{gradient} = 70-30$, uniform porosity $\phi = 0.50$).
- Fig. 16 shows plot of x velocity along the lines in midplane of the space between brood chamber and honey super (Line L2) for different runs from #4 to #7 ((a)–(d)) done in Case C. We can clearly see the mixing pattern change depending upon the porosity variation between the honeybee clusters.
- Fig. 17 shows the plot of z velocity contours on different XZ cross-sections cutting the air space below the brood chamber where (a) is closest to the inlet plane and (f) closest to the wall farthest from the inlet and rest at increasing distances from the inlet. In this figure, we can clearly see that there are vortices in the space below the frames aligned under neath the frames. These vortices were illustrated in one of the pathlines shown in the figure in the paper.
- Figs. 18 and 19 show the vector plots on a YZ plane cutting through the middle of different bee cover volumes in a beehive with $\beta_{gradient} = 70-30$ at $T_{amb} = 20.0^\circ\text{C}$ in Fig. 18 and at $T_{amb} = 27.5^\circ\text{C}$ in Fig. 19. In each figure the sub-figures (a)–(d) correspond to bee cover volumes 1 to 4 respectively. We can clearly see from $T_{amb} = 27.5^\circ\text{C}$ vector plots, that flow enters only half way into the beehive and it looks very different from the one seen for $T_{amb} = 20.0^\circ\text{C}$ case.

Appendix B. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jtbi.2011.11.007.

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