TECHNICAL ARTICLE

A Review on Thermoregulation Techniques in Honey Bees’ (Apis Mellifera) Beehive Microclimate and Its Similarities to the Heating and Cooling Management in Buildings

Hasila Jarimi, Emmanuel Tapia-Brito and Saffa Riffat

Apis mellifera – Apis, which is Latin for ‘bee’, and mellifera, which is Latin for ‘honey-bearing’ – refers to Western or European honey bees. Research shows that regardless of the ambient temperature, the in-hive microclimate of a beehive at the central brood area must be kept at the average optimum temperature of 35 °C for the colony to survive. Therefore, to survive both cold winters and hot summers, Apis mellifera will employ several heating and cooling strategies to thermoregulate their hives at the optimum temperature. Just like beehives, our buildings are designed with an envelope that is frequently viewed as the barrier that protects the internal occupied space from the impact of the external environment. We also employ similar methodologies to thermoregulate our buildings to reduce the heating and cooling load for less energy consumption while at the same time providing thermal comfort to the occupants. This paper presents the thermoregulation techniques employed by honey bees and the similarities to our buildings. Many similarities can be seen between the honey bees’ hive and our buildings’ thermal management system. However, we can still learn from the thermoregulation management demonstrated by the honey bees.

Keywords: Thermoregulation techniques; Beehives; Human buildings; Apis mellifera

1. Introduction

A honey bee is an insect that has three main parts to its body: head, thorax and abdomen (Ivor Davis and Roger Cullum-Kenyon, 2018). A colony of a beehive typically consists of a single queen bee; 10,000–60,000 female worker bees that are in charge of cleaning, nursing and serving the broods, foraging, transferring nectar, making the wax, and guarding their colony; and 1000–2000 male bees (drones) in the summer with the only task of mating with a virgin queen from a foreign colony (R. Christopher Mathis and David R. Tarpy, 2007, Ivor Davis and Roger Cullum-Kenyon, 2018). Figure 1 illustrates the three types of bees living in a colony with their average size. The bees’ nest or beehive is where a colony resides or is physically

Figure 1: (Left) three types of bee in a colony and their relative size (Christopher M. Jernigan, 2017); (right) worker bees constructing honeycomb wax mage by Charles Kazilek as in (Christopher M. Jernigan, 2017).

* Department of Architecture and Built Environment, Faculty of Engineering, University of Nottingham, University Park, Nottingham, UK
† Solar Energy Research Institute, Universiti Kebangsaan Malaysia, Bangi, MY
Corresponding author: Hasila Jarimi (H.jarimi@gmail.com)
located. In the hive, worker bees will construct a honeycomb, which is a mass of hexagonal prismatic wax cells, for the queen bee to lay eggs and for the worker bees to store their honey and pollen. Creating the wax comb is said to be energetically costly. Secreted from the worker bees’ stomach, the production of wax requires at least 6 grams of sugars in the form of honey for every gram of wax secreted (R. Christopher Mathis and David R. Tarpy, 2007). During the process, the worker bees will cluster together to increase their body temperature to 37 °C. The secreted wax will be chewed to make the wax ‘workable’ and shaped into the typical hexagon shapes that fit neatly or stick together.

2. In-Hive Thermoregulation Techniques of the Honey Bees And The Similarities To Human Dwellings

Just like beehives, human buildings were designed in such a way that the envelopes are frequently viewed as the barrier that protects the internal occupied spaces from the impact of the external environment, such as sun, wind, rain and snow. We also employ similar methodologies to thermoregulate our buildings to reduce the heating and cooling load for less energy consumption. A heating, ventilation and air conditioning (HVAC) system is what humans rely on to provide the conditions that we need, such as a certain temperature, relative humidity and ventilation, to ensure the health and thermal comfort of the occupants.

Apis mellifera – Apis, which is Latin for ‘bee’, and mellifera, which is Latin for ‘honey-bearing’ – refers to Western or European honeybees. Research shows that regardless of the ambient temperature, the in-hive microclimate of a beehive at the central brood area must be kept at the average optimum temperature of 32 °C–36 °C for the colony to survive (Seeley T.D. and B., 1981). Therefore, to survive both cold winters and hot summers, just like human buildings,Apis mellifera will employ several heating and cooling strategies to thermoregulate their hives at the optimum temperature. Humans have studied honey bees since 7000 BC. It is possible that humans have been inspired by honey bees and learned from them in creating thermal comfort in our buildings in a sustainable way. In this paper, we will explore and discuss various aspects of thermal comfort management of a honey bee colony, including heating, cooling, humidity control, and in-hive air quality. The similarities of the thermal management strategy to the human dwellings that reflect what humans could have learned or can learn from honey bees are discussed.

2.1. Heating in winter or during cold weather

Table 1 below summarises the temperature ranges and the state of the honey bees when exposed to different temperature ranges. To provide heating in cold conditions, like the honey bees, from an endothermic perspective, buildings will consume energy or fuel to create stable thermal comfort. To survive the cold winters, the European bees employ several heating strategies, which include air gap sealing, clustering to create insulation, and endothermic heating, to maintain their beehive at its optimum temperature.

2.1.1. Air sealing to reduce heat leakage

For millions of years, honey bees evolved in tree hollows, which are perfectly insulated with the surrounding wood. Living at a thermally insulated ambient temperature is very common for honey bees. However, modern beehives do not have such insulation, and therefore the honey bees will instinctively reduce any possibility of heat loss due to the following: i) an unwanted cavity, ii) air draught heat loss, iii) large entrance or gaps, and iv) unwanted air flow in winter. To do that, as can be seen in Figure 2, honey...
bees will use propolis, a sticky wax-like resin that acts like superglue, to seal all the cracks and gaps and any forms of opening in the hive. However, since the air flow from the entrance is required for ventilation, honey bees will decide when to close the entrance. Typically, the sealing process takes place in autumn (Hudston, 2017). The propolis at the hive’s entrance is also used as the defence against robber bees and mice, for example.

Heat loss from buildings can occur through gaps and cracks around windows, doors and roofs through air leakage (please see Figure 3). Gaps in insulation and thermal bridging are also a substantial source of heat loss and can cause both draughts and condensation. Regardless of how well a house is insulated to reduce heat loss and heat gain, a proportion of energy is still lost to draughts caused by air leakage. Research shows that building air leakage can cause as much as 15−25% of winter heat loss in buildings and can contribute to a significant loss of coolness in climates where air conditioners are used since the energy used to heat or cool our buildings leaks through unwanted draughts (Chris Reardon, 2013). In addition to heat loss, air leakage can cause condensation that will damage the building materials and reduce indoor air quality. Honey bees use propolis for air sealing, and this technique should sound familiar to any house builders or homeowners. To avoid air leakage, they will use airtight construction while ensuring that junctions and gaps between building components such as at the window and door frames, walls, floors and ceilings, skirting boards, plumbing pipes, exposed rafters and beams, inbuilt heaters and air conditioners, and between dissimilar materials (e.g. masonry walls and timber framing) are sealed with durable, flexible caulks and seals. Larger gaps will be sealed with expandable foam.

2.1.2. Heat insulation and endothermic heating
When the temperature drops to 15 °C, the bees will start to cluster (Southwick and Heldmaier, 1987). The bees will form a compact cluster (please see Figure 4a), where bees position themselves in layers, clumping together oriented inward to reduce the in-hive volume of air for heating.

![Figure 3: Thermal infrared images that show heat leakage from different parts of a house. Image taken from (Ahomcheck, 2018).](image)

![Figure 4: (a) Winter clustering in a beehive (Oliver, 2016) (b) an illustration of European honey bees clustering together in a mass to generate and conserve heat (Purdue Extension, 2017); (c) infrared thermogram of the bees on the central comb of a broodless winter cluster (Stabentheiner et al., 2003).](image)
Obeying the principle of heat transfer that increases with the increase in surface area, the cluster formation will reduce the bee bodies’ surface area exposed to the cold air, thus reducing heat loss via convection by as much as 88% (Southwick, 1983). As the ambient temperature drops, the cluster will become tighter and more compact (less porous), thus further reducing the internal convection current by closing the air channel for ventilation (Southwick, 1983).

Home builders also employ this strategy of reducing the air volume needing heat in a building or house by creating buffer zones as foyers to help to reduce heat loss to the outside. The HVAC system was designed to allow for zoning and partial or complete shutdown of supply to minimise the heating area (R. Christopher Mathis and David R. Tarp, 2007). There can also be some utility areas in a building that have lower temperature requirements due to the nature of their functions or the period of their use. Therefore, these zones are suitable for the creation of thermal buffers that would reduce static heat loss in spaces where the maintenance of higher temperatures is important for thermal comfort.

Figure 4b illustrates the bees’ orientation in the winter clustering. It mainly consists of three layers. In the interior of the cluster, the heater bees will perform ‘endothermic heating’, whereby an individual bee produces metabolic heat via its thoracic flight muscles due to the involuntary muscle contractions (shivering). The heater bees generally remain motionless. To dissipate the heat in the cluster and regulate the amount of CO$_2$, a group of bees will fan their wings to ventilate the heated air. To shield the cluster from heat loss, on the external surface of the cluster other bees will connect their legs together to form a shell. Functioning like an insulation layer for a building envelope, this mantle of bees will keep the warmth inside the cluster with their overall heat conductance of approximately 0.10 W/kg °C. As the temperature drops further, to below –10 °C, the bees will increase their endothermic heating to stay warm, which is indeed hard work for the bees. The centre of the cluster basically serves as the central heating system for the colony. The individual bees take turns to perform endothermic heating, fanning, and serving as mantle bees. They rotate in and out of the cluster protecting the queen and keeping the brood nest area warm and safe (Purdue Extension, 2017). Figure 4c shows the thermal infrared image which reflects the temperature variation from the centre of the winter cluster to the surface of the cluster forming a thermal mass wall to the centre of the hives or the brood comb (Stabentheiner et al., 2003). Furthermore, the bees’ body hairs help to enhance the effectiveness of the insulation of the winter cluster. A bee’s body hairs are not only useful to hold pollen, but also in a winter cluster, the hairs have a heat retention property in trapping heat to reduce heat escaping from their body.

Just like honey bees, humans have employed a building envelope heat insulation strategy to reduce heat loss to the cold. In recent years, high-insulating and fire-safe insulating materials have been actively researched. As mentioned earlier, honey bees will increase their Endothermic heating based on the drop in the temperature. We have also incorporated a ‘heating’ system by installing a single centralised thermostat to monitor a room’s temperature, whereby heating will only be introduced when the internal space temperature drops to a certain level. However, unlike honey bees that employ a decentralised control system, human beings have mainly employed a centralised control system like a thermostat to control the HVAC system in a building. In a beehive decentralised heating system, collective decision-making based on individual honey bees’ assessment of what needs to be done (i.e. heating, fanning or shielding) regarding the immediate local temperature and humidity allows any form of disturbance or perturbations in the in-hive environmental conditions to be addressed very quickly via communication among the bees. This is possible because the bees are not relying only on one single temperature point to respond, but rather on multiple and redundant individual honey bees.

2.2. Cooling during summer or in hot weather
The 35 °C in-hive optimum temperature also applies in a warm environment. To survive in warm temperatures, bees have employed a cooling mechanism. Naturally, the bees’ cluster disperses at a temperature above 15 °C to reduce heat insulation. At a time of high ambient temperature conditions, which happens mainly in the summer, during the daytime, overheating due to overcrowding is unlikely to happen because most of the worker bees are on foraging and drones are also outside the colony. Moreover, at night-time, if the hive is overcrowded, the bees will instinctively hang outside in front of their hive’s entrance, spending the night outside and staying cool. Nevertheless, to ensure that the brood nest is maintained at its optimum temperature, several cooling strategies have been employed by the worker bees in the beehive.

2.2.1. Ventilation and cooling
To cool the beehive, bees will ventilate the hive by actively fanning their wings. In a research study conducted by (Southwick and Moritz, 1987), when the air temperature inside the brood nest was approaching 35 °C, several hundred bees positioned themselves throughout the beehive (i.e. left, right, top and bottom) to take up the fanning position in the ventilation process. These bees, which are called fanners, force air circulation throughout the beehive. However, as the temperature increased to above 40 °C, 20–30 bees moved to the outside of the small entrance into the screened landing platform and began fanning activities. These fanning bees also employed a ventilation strategy where they organise themselves into groups and separating regions of continuous inflow and outflow at the hive’s entrance. Figure 5a shows the schematic illustrating the path of air through the hive as induced by fanning bees. The warm stale air fanned out from the hive will be replaced/exchanged with cooler fresh air from external ambient hat will enter passively into the hive where fanning bees are absent (Peters et al., 2019). It is also very important to note that during the air exchange, sufficient gaseous exchange of oxygen and CO$_2$ and control of humidity will also be taking place. Similar to honey bees, in hot weather conditions,
the key to cooling a building is removing the built-up heat in the house. This is achievable by using either a natural ventilation system or, like fanner worker bees, a forced mechanical ventilation system that can be introduced to replace the unwanted heat with a cooler fresh air supply. An example very similar to the fanning system introduced by the honey bees at the hive entrance is the window fan that expels hot/stuffy air from an internal space that is then replaced by cooler fresh air from outside (see Figure 5b). Other types of fans and ventilation systems are attic fans, large ceiling air-circulating fans, whole-house fans, and the typical exhaust fans installed in a kitchen, bathroom, etc. to move hot moist air from indoors to outdoors.

2.2.2. Heat shield
Another strategy implemented by honey bees in protecting their broods is via heat shielding whereby the worker bees absorb heat by pressing the ventral side of their bodies against the heated surface (Bonoan et al., 2014). The bees will later on fly away to area in the beehive that is cooler than the brood area and dissipate the absorbed or stored heat. A similar strategy has been employed by homebuilders via double skin facade of a building whereby the first external layer performs as the exterior wall meanwhile, the second layer perform as the insulation layer avoiding heat from entering the building by heat remval through air ventilation, just like the bees that removes the absorbed heat to a cooler area.

Also employing a similar heat shield or heat absorption strategy, researchers (Bermejo-Busto et al., 2016) proposed an industrial-scale modular active ventilated facade prototype with a new Thermoelectric Peltier System. In the proposed design, the Thermoelectric Peltier System extracts the overheating from the room to the air cavity. On the other hand, during cold seasons the inverse process takes place (Bermejo-Busto et al., 2016).

2.2.3. Evaporative (swamp) cooler
Another method of cooling employed by honey bees is evaporative cooling with the working principle just like the well-known evaporative cooler or ‘swamp cooler’. The working principle of the evaporative cooling system that is very similar to the honey bees in cooling their beehive is shown in Figure 6. To perform evaporative cooling, worker bees will spew the water that they carried to the beehives in their bodies. Other worker bees will then start fanning, actively creating cool humid air that circulates throughout the beehive. Honey bees naturally know that cool air drops, and therefore the water is normally spewed from the top, under the beehive lid.

2.2.4. Humidity and air quality control
In addition to the temperature, the bees team up to maintain different humidity levels in the different parts of the hive mainly via an air ventilation mechanism. Similar to our buildings, air ventilation in a beehive is not only important to expel the heat build-up in a house to avoid overheating, as mentioned earlier, but also to reduce the CO₂ concentration and water vapour and exchange them with a fresh supply of oxygen (Sudarsan et al., 2012) for better air quality. A wet and damp beehive, especially the build-up of condensation due to the humid air, can lead to unwanted mould forming in the centre of the brood comb area. It has been concluded that a honey bee colony has the ability to regulate the humidity in its hive regardless of the weather conditions throughout the year (Eouzan et al., 2019). In a research study conducted by (Sachs and Tautz, 2017), in cold weather at an average floor temperature of 10 °C, the humidity level is well controlled at a constant temperature. The only possible explanation is that there is a change in the air within the hive with the same temperature but different relative humidity via the active ventilation process performed by the honey bees. In the first step, the bees will fan cold air into the beehive via one of the edges, the cold dry air will warm up and increase
in humidity, and then the warm humid air will be fanned downwards. As a result, the cold air from the hive’s floor will become humid. However, the bees located above and at the side walls of the centre of the comb act as the heat exchanger. Just like a dehumidifier, the bees will heat the cold humid air and turn it into ‘dry’ air that is then fanned into the centre of the comb. This temperature and relative humidity control technique is very similar to a mechanical ventilation and heat recovery unit in a building. In addition to ventilation to ensure healthy hives, scientists have discovered that honey bees have sterilised their hives with propolis, which gives the whole colony what is considered to be a form of social immunity. Propolis was found to have certain desirable antibacterial and antifungal properties for colony hygiene (R. Christopher Mathis and David R. Tarpy, 2007). In our buildings, indoor air quality control has recently attracted more interest from researchers. Indoor air qualities involves the control of the CO₂ level in a building, as well as other gases such as carbon monoxide, volatile organic compounds, particulates, and microbial contaminants (mould, bacteria). The common indoor air quality system involves filtration and the use of ventilation to dilute contaminants.

### 3. Discussion and conclusions

Many similarities can be seen between the honey bees’ hive and our buildings’ thermal management system, as summarised in Table 2. However, we can still learn from the thermoregulation management demonstrated by the honey bees, for example, the fact that the temperature stability of the beehive has been very consistent and well maintained regardless of the ambient climate. This is owing to the decentralised and collective decision-making employed by a honey bee colony. The worker bees in a colony are not being ‘allocated’ tasks in any way. However, any form of disturbance or changes detected in the hive’s environment are individually assessed by each of the worker bees and then immediately passed to the other bees through their special communication technique, ‘chemical communication’, via the pheromones secreted

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**Figure 6:** (a) Evaporative (swamp) cooler working principle. Image taken from (Richmueller, 2012); (b) an illustration of evaporative cooling performed by the worker bees.

**Table 2:** The similarities between beehives’ thermoregulation strategy and our buildings.

| Thermoregulation techniques       | Beehives                                                                 | Buildings                                                                 |
|-----------------------------------|--------------------------------------------------------------------------|--------------------------------------------------------------------------|
| Increase insulation               | Air sealing using propolis, and winter cluster with mantle bees as the heat shield | Seal gaps, cracks at windows, doors, roof area – air tightness testing    |
|                                   |                                                                          | Advance heat insulation layer                                             |
| Efficient heating                 | Decentralised control system and endothermic heating only initiated by the bees when the temperature drops further and when clustering can no longer retain heat | Thermostat to monitor heating system and room temperature                |
| Reduce volume of air for heating  | Cluster is formed inward surrounding the central brood area              | Buffer zones, thermal buffers                                             |
| Efficient ventilation and cooling | Honey bees employ fanning by repositioning themselves and employ evaporative cooling by spewing water from the top | Air ventilation system and evaporative cooler technology                  |
| Indoor air quality and hygiene control | Efficient ventilation system with honey bees sterilising their beehives with propolis | Air filtration and ventilation system to control indoor air quality       |
| Humidity and temperature control  | In certain temperature conditions, the side wall bees perform like a heat exchanger | Efficient heat recovery units                                              |
by the bees and their special dance language, known as waggle dance or wag-tail dance. We can compare this to the heating and cooling control system of a house with tens or hundreds of installed integrated thermostats. A heating or cooling system in a house mainly has a centralised control that has a slow response and feedback and is highly variable but with less energy and capital cost consumption. Nevertheless, human beings have indeed employed several decentralised control strategies in buildings, which include the use of a motion sensor lighting system to reduce lighting loads in non-used space.

Clearly, for over million years, honey bees have shown that they employ an excellent thermoregulation strategy for their hives. However, as extreme cold weather conditions and heatwaves have become more and more common due to climate change or global warming, whether Apis mellifera can easily adapt themselves in maintaining an efficient in-hive thermoregulation technique is questionable. Another question to consider is how climate change will impact on the honey bees’ behaviour, physiology and distribution, and on the evolution of the honey bees’ interaction with diseases. Whether they will need extra help from us is a question that is worth addressing in future research.

Acknowledgements
The authors gratefully acknowledge Innovate UK’s financial support through project number 105403.

Competing Interests
The authors have no competing interests to declare.

References
Ahomecheck. 2018. Air leakage testing [Online]. Available: http://ahomecheck.ca/air-leakage-testing [Accessed].

Backyardhive. 2017. BEES ADD PROPOLIS TO THEIR HIVE ENTRANCE TO WINTERIZE AND DEFEND FROM ROPPER BEEs. [Online]. Available: https://backyardhive.com/blogs/managing-your-top-bar-hive/propolis-the-defender-of-the-hive [Accessed].

Bermejo-Busto, J, Martín-Gómez, C, Zuazua-Ros, A, Ibáñez-Puy, M, Miranda, R and Baquero Martín, E. 2016. Improvement of an integrated Peltier HVAC system integrated using beehive and stigmergy strategies/Mejora de un sistema de climatización con células Peltier a partir de la colmena de abejas: una aproximación teórica. DYNA INGENIERIA E INDUSTRIA, DYNA-ACELERADO. DOI: https://doi.org/10.6036/7865

Bonoan, RE, Goldman, RR, Wong, PY and Starks, PT. 2014. Vasculature of the hive: heat dissipation in the honey bee (Apis mellifera) hive. Naturwissenschaften, 101: 459–65. DOI: https://doi.org/10.1007/s00114-014-1174-2

Davis, I and Cullum-Kenyon, R. 2018. The BBKA guide to beekeeping. London: Bloombury Wildlife.

Eouzan, I, Garnery, I, Pinto, MA, Delalande, D, Neves, CJ, Fabre, F, Lesobre, J, Houte, S, Estonba, A, Montes, I, Sime-Ngando, T and Biron, DG. 2019. Hygrocetulation, a key ability for eusocial insects: Native Western European honeybees as a case study. Plos one, 14: e0200048-e0200048. DOI: https://doi.org/10.1371/journal.pone.0200048

Hubbard, B. 2019. The 10 Best Window Fans [Online]. Available: https://www.thearchitectsguide.com/articles/best-window-fan [Accessed 10 November 2019].

Hudston, S. 2017. The bees are already sealing their hives for the winter ahead [Online]. The Guardian. Available: https://www.theguardian.com/environment/2017/aug/26/country-diary-bees-sealing-hives-propolis [Accessed 20 July 2019].

Jernigan, CM. 2017. Bee Colony Life [Online]. Arizona State University School of Life Sciences Ask A Biologist. Available: https://askabiologist.asu.edu/beecolony-life [Accessed November 10 2019].

Just Bee. 2019. What is propolis. Available from: https://www.justbeedrinks.co.uk/propolis-can-help/ [Accessed].

Mathis, RC and Tarpy, DR. 2007. 70 Million Years of Building Thermal Envelope Experience: Building Science Lessons from the Honey Bee.

Oliver, R. 2016. The Physics Of The Winter Cluster [Online]. American Bee Journal. Available: http://scientificbeekeeping.com/understanding-colony-buildup-and-decline-part-13a/ [Accessed 10 November 2019].

Peters, JM, Peleg, O and Mahadevan, L. 2019. Collective ventilation in honeybee nests. Journal of The Royal Society Interface, 16: 20180561. DOI: https://doi.org/10.1098/rsif.2018.0561

Purdue Extension. 2017. THE COMPLEX LIFE OF THE HONEY BEE [Online]. Available: https://www.purdue.edu/resources/ppp-publications/the-complex-life-of-the-honey-bee/ [Accessed].

Reardon, C. 2013. Sealing your home. Available: http://www.yourhome.gov.au/sites/prod.yourhome.gov.au/files/pdf/YOURHOME-PassiveDesign-SealingYourHome.pdf.

Richmueller. 2012. D.I.Y. Inspired Evaporative Cooler Design for Remote Military Applications [Online]. Available: https://muellerdesignlab.wordpress.com/2012/04/20/evaporative-cooler-design/ [Accessed].

Sachs, R and Tautz, J. 2017. How Bees (Apis Mellifera) Reduce Humidity in the Beehive by Means of Active Ventilation.

Seeley, TD and B., H. 1981. Insects thermoregulation. New York: Wiley.

Southwick, EE. 1983. The honey bee cluster as a homeothermic superorganism. Comparative Biochemistry and Physiology Part A: Physiology, 75: 641–645. DOI: https://doi.org/10.1016/0300-9629(83)90434-6

Southwick, EE and Heldmaier, G. 1987. Temperature Control in Honey Bee Colonies. BioScience, 37: 395–399. DOI: https://doi.org/10.2307/1310562

Southwick, EE and Moritz, RFA. 1987. Social control of air ventilation in colonies of honey bees, Apis mellifera. Journal of Insect Physiology, 33: 623–626. DOI: https://doi.org/10.1016/0022-1910(87)90130-2
Stabentheiner, A, Pressl, H, Papst, T, Hrassnigg, N and Crailsheim, K. 2003. Endothermic heat production in honeybee winter clusters. Journal of Experimental Biology, 206: 353. DOI: https://doi.org/10.1242/jeb.00082

Sudarsan, R, Thompson, C, Kevan, PG and Eberl, HJ. 2012. Flow currents and ventilation in Langstroth beehives due to brood thermoregulation efforts of honeybees. Journal of Theoretical Biology, 295: 168–193. DOI: https://doi.org/10.1016/j.jtbi.2011.11.007