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Ratios of colony mass to thermal conductance of tree and man-made nest enclosures of *Apis mellifera*: implications for survival, clustering, humidity regulation and *Varroa destructor*

Derek Mitchell[1]

Abstract In the absence of human intervention, the honeybee (*Apis mellifera* L.) usually constructs its nest in a tree within a tall, narrow, thick-walled cavity high above the ground (the enclosure); however, most research and apiculture is conducted in the thin-walled, squat wooden enclosures we know as hives. This experimental research, using various hives and thermal models of trees, has found that the heat transfer rate is approximately four to seven times greater in the hives in common use, compared to a typical tree enclosure in winter configuration. This gives a ratio of colony mass to lumped enclosure thermal conductance (MCR) of less than 0.8 kgW^{-1} K for wooden hives and greater than 5 kgW^{-1} K for tree enclosures. This result for tree enclosures implies higher levels of humidity in the nest, increased survival of smaller colonies and lower *Varroa destructor* breeding success. Many honeybee behaviours previously thought to be intrinsic may only be a coping mechanism for human intervention; for example, at an MCR of above 2 kgW^{-1} K, clustering in a tree enclosure may be an optional, rare, heat conservation behaviour for established colonies, rather than the compulsory, frequent, life-saving behaviour that is in the hives in common use. The implied improved survival in hives with thermal properties of tree nests may help to solve some of the problems honeybees are currently facing in apiculture.

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Introduction

Honeybees (*Apis mellifera* L.) are a well-researched organism that regulates their colony temperature through variable heat generation (Simpson 1961; Southwick 1985) and variable colony conductance (i.e. clustering). They do not hibernate in winter, maintaining some part of the colony above 18 °C all year, yet their natural geographical range extends to cool temperate regions and uses differentiation to cope with the cooler climates (e.g. *Apis mellifera iberiensis* versus *Apis mellifera jemenitica* (Franck et al. 1998; Hossam 2012)). The honeybees' original nest enclosure is usually a tree with tall, narrow, thick-walled cavity (see Fig. 1) (Seeley and Morse 1976). They prefer entrances towards the bottom of the cavity (Seeley 1985). They close up any small holes and seal the cavity surface with plant resins of low water vapour permeability (i.e. propolis) (Seeley 1985). Honeybees gain thermal advantage in cool climates by constructing their wax combs from the top of the cavity downwards, retreating upwards when they need to conserve heat (Owens 1971) (*Apis mellifera ligustica*) and expanding downwards as the colony grows and increases its heat and honey production (Crane 1990, p. 90). However, most research is conducted at either constant temperature laboratory conditions (Stabenthiener 2010; Williams 2013) or in squat (~200 mm in height) wide (~450 mm × ~450 mm) hives (Delaplane et al. 2013), with wooden walls typically 13 to 19 mm in thickness (Cushman 2011). This allows only very limited vertical movement of the

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Fig. 1 Relative sizes of tree nest enclosures, hives and tree models (m)
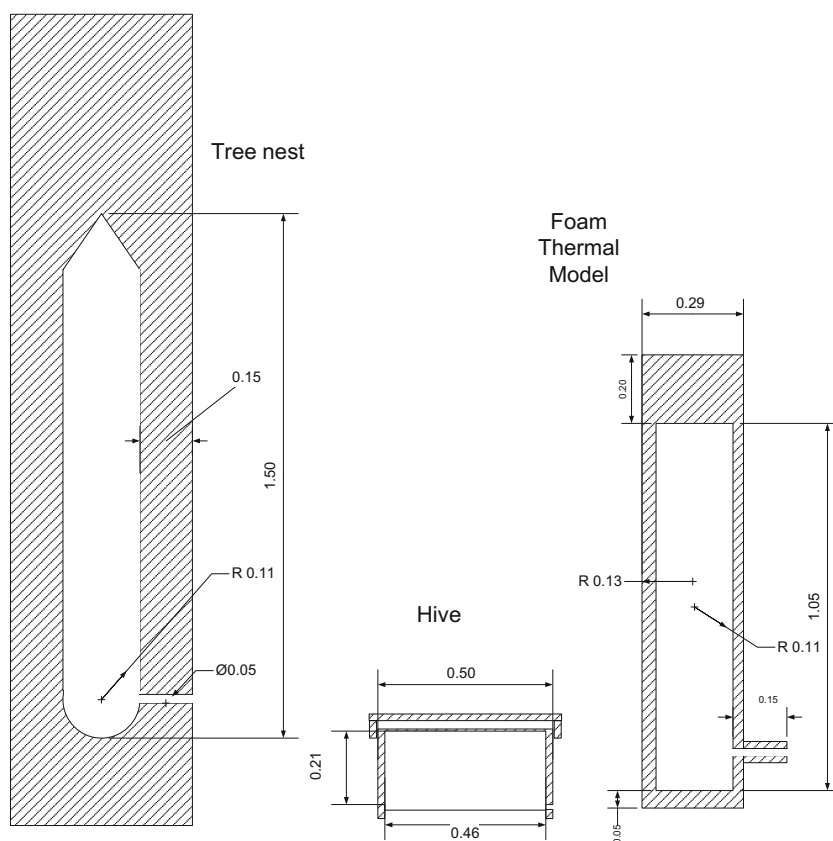
colony. As a consequence, studies may not take into account honeybee behaviours that are expressed or altered in a thermal environment similar to a tree nest.

In almost all studies of honeybees that do use insulated enclosures, the conductance has not been measured and, in all cases, is estimated (from material thickness or onset of clustering) to be considerably less insulated than in tree enclosures (Owens 1971; Ptáček 2000; Olszewski 2007; Erdogan 2009; Villa 2009). Some researchers have studied the thermal properties of tree cavities in relation to other animals, but many have not quantified the temperature rise in relation to heat input (Buttemer 1985; Coombs et al. 2010; Maziarz and Wesołowski 2013). Two studies of heat transfer in tree cavities tie their models to animals in conductive contact at the bottom of the nest (Thorkelson and Maxwell 1974; Fornito et al. 1982), and although there has been some speculation on the difference in the conductance between man-made hives and tree enclosures (Erickson 1990), I have found no attempts at a measurement-based comparison of heat transfer rate of the various types of honeybee enclosures.

To maintain temperature homeostasis in a cool environment, energy lost through the nest enclosure must be made up by more honeybee activity and stress, either to generate more heat or to cluster. This can affect nest humidity, colony survival, spring development and honey production (Villumstad 1974). Higher nest temperatures

and humidity have been linked to reductions in disease and parasites (Flores et al. 1996; Kraus and Velthuis 1997; Tamashbi 2009; Flores 2011; Chen et al. 2012; Hossam 2012).

This study experimentally investigates the important physical characteristic, the lumped thermal conductance of the enclosure, for a thermal model of tree nest enclosures in winter configuration and hive types commonly used in apiculture and research. It then derives from the heat transfer equations, a key factor in determining nest temperature (colony mass-to-lumped enclosure conductance ratio (MCR)). Using this factor, the study relates it to the key metabolic rates and temperatures of intact honeybee colonies in the enclosures studied.

The Langstroth and British National hives tested are ones commercially available in the UK. However, their design, construction and materials are typical of removable frame and box hives used throughout the world. A particular study was made of hives constructed from expanded polystyrene (EPS), and samples were successfully sought from all of the major suppliers of EPS hives in the UK.

The objectives of this research were as follows:

- To enable researchers and beekeepers to establish a norm for heat transfer, for research and apicultural purposes.
- To put honeybees' behaviour into their original nest enclosure context.

- To enable better informed design decisions for the construction of hives and research experiments.

Materials and methods

A tree enclosure as surveyed (Seeley and Morse 1976) can be considered as an insulated hollow tube, sealed at the top with massive insulation and partially open at the bottom, with a suspended distributed heat source that can be placed at varying heights within it. Such a system has strong convection above and around the heat source as well as some stratification and weaker convection below the heat source mixing with outside air (Owens 1971). In contrast, commercially available beehives are squat, relatively thin-walled boxes of various sizes and configurations, often with metal mesh floors, and relatively thin roofs (Cushman 2011). These hives allow only very limited vertical movement of the heat source. Cross sections of these items, with typical dimensions, are shown in Fig. 1. To compare the thermal conductivities of these very different enclosures, an experimental approach was chosen which concentrates on the region in and above where the honeybee colony resides in winter (Owens 1971).

Scope, assumptions and simplifications

The experimental scope is to determine the lumped thermal conductance of the enclosures and is simplified by the following:

- Considering only free energy at equilibrium in still air, and constant ambient temperature, transient effects of heat capacity of the nest and the enclosure as well as forced convection, evaporation and condensation are thus eliminated.

  The heat capacities of the nest and the amount of metabolic vapour are dependent on the behavioural reaction to the enclosure and thus outside the scope of the experiment. The heat capacities of enclosures are not investigated due to the practical difficulties created by the high heat capacity of the tree.

- The internal nest structure is treated as an impermeable 'black box' with a distributed boundary spanning the region where the honeybee colony resides in winter, which heats the air between the nest and the enclosure, which then, by natural convection, heats the enclosure, which, in turn, is cooled by natural convection in the outside environment.

  This ensures that the results reflect the contribution from the enclosure and not the nest contents, which are largely constructed by the honeybees. These should therefore be studied as part of the honeybee behaviour reacting to the properties of the enclosure; for example, clusters form in

corners in EPS hives while they remain in the centre of wooden hives. This experiment is aimed at providing the foundation to that behavioural work and, therefore, does assume any specific disposition of comb and stores and honeybees.

- The enclosures have openings only at the bottom, and the rest of the enclosure is impermeable to air movement.

  This is justified by the following:

- It is the lowest energy loss configuration (Kraus and Kubečková 2013).
- Honeybees seek out lower entrances and attempt to seal up small openings in the rest of the nest (Seeley 1985).
- Recent research on the fluid dynamics of displacement ventilation has shown this to be significantly more complex (Lin and Xu 2013; Linden 1999) than earlier apidology research (Anderson 1948) had suggested.

Approach

The method adopted was to heat a honeybee enclosure with a known power input, comparable to a honeybee colony input, from a heat source suspended in the cavity. Then, the temperature gradient was observed at equilibrium using vertical arrays of 12-bit digital thermometer integrated circuits (ICs), MicroChip® TCN75A (Microchip Inc n.d.), spaced at 57 mm intervals, referenced to the highest part of the cavity where comb could be placed by honeybees. These sensors were connected to a computer-based data acquisition system. The power output (20 W) for the resistive heating was chosen to be equivalent to the consumption of 10 kg of sucrose over 100 days and approximates the 20 °C peak metabolic output of a 1 kg colony of honeybees (Southwick 1982) and was measured using two IEEE-IB Solartron digital 7150 plus multi-meters. A range of power inputs was necessary as both foam and wood vary in conductivity with temperature (Bogdan et al. 2005), and therefore, the maximum temperature rise of the foam models was constrained to be between 25 and 10 °C. As the wooden removable frame hive had such a low increase in temperature, a further measurement at 34 W was taken, a value equivalent to 1.7 kg of honeybees. In addition, these characteristics were compared to a calculated conductance per unit height.

Tree model

The heat capacity of a 1.5 m high tree enclosure would be of the order of 200 kJ K^{-1} (The Forest Products Laboratory 2010). This would take over 30 h to rise by 10 °C without considering heat losses. It was therefore decided to make full-size low-thermal capacity, equivalent conductance, models of the tree enclosures. These were constructed in

polyisocyanurate (PIR) foam sheet as hexagonal tubes to approximate wooden cylinders.

The thermal models were constructed with dimensions and thickness of sheet to give the required conductance per unit height 'U values' WK^{-1} m^{-1}, using the following:

- The thermal conductance shape factors of 6.92 for a hexagonal tube (calculated from the integration of Fourier's law (Incropra et al. 2006)) and 6.28 for a cylinder.
- The tree survey conducted by Seeley and Morse (Seeley and Morse 1976) was used to provide species and dimension distributions.
- Standard bulk wood thermal conductivity (λ) at 12 % water content (The Forest Products Laboratory 2010).
- PIR sheet conductivity (Bogdan et al. 2005).

The thermal models of the tree enclosure constructed are listed with the hive types tested in Table 1. The tree models were constructed with an entrance tube to simulate the longer length of the entrance through the wood of the tree. The tree models were glued, tape sealed inside and out and constructed in modular lengths so that different heights and, therefore, volumes could be tested. The top of the model was capped with 200 mm of PIR to take the place of the rest of tree above the nest.

Method

The heating element was suspended so that the bottom of the element was at the same distance from the top of the empty model/hive, i.e. 200 mm. This was to ensure a similar thermal stratification and churning and to emulate the presence of a honeybee cluster ~200 mm in diameter, the maximum diameter of a sphere that will fit inside a British National hive and still be in contact with the comb. The measurement sensors were arranged so that the highest element was within 10 mm of the top of the cavity. The enclosure was then heated either with 20 W or a lower value for a number of hours to establish equilibrium conditions, while air temperatures within the enclosure (T_{nest}) and in the ambient environment (T_{external}) were logged every 10 s.

In the hives The heater (with radiant heat shield) and sensors were placed in separate frames placed at one third and two thirds the distance across the box, respectively. The sensors were mounted in the frame on two vertical printed circuit boards (PCBs), each with four temperature sensors. The PCBs were spaced at one third and two thirds the distance across the frame. The hive crown boards or roofs were carefully sealed with adhesive tape. Any entrance block supplied with the hive was inserted to allow the minimum entrance space for the honeybees. Any crown board openings were closed and sealed. The roofs were weighted (15 kg) to compress the

components of the hives together to further improve the sealing. Experimental runs were repeated before and after sealing to ensure the efficacy of the sealing methods.

In the foam tree models The sensor PCBs were attached to a central 32 mm plastic tube one above the other. The heater was suspended with its heat shield on the far side of the tube from sensors. Glue sealants were used to eliminate leakage and, therefore, heat loss from the top of the model.

In the fifth scale wood cylinder model A single temperature sensor was inserted 19 mm from the top of the cavity, opposite to a shielded heater, 38 mm in height. The heater was supplied with 1.5 W so that the sensor indicated circa 30 °C. The resulting heat transfer rate was scaled by one fifth to allow for the smaller height of cylinder heated.

Results

The average thermal conductivity (λ) of the wood in the tree nest survey (Seeley and Morse 1976) was calculated to be 0.153 ± 0.05 Wm^{-1} K^{-1} (including 20 % uncertainty of λ in the original species) by weighting each species by its percentage presence in the survey. This value of λ was then used with the diameter and entrance length from the same survey using the shape factor to give a resultant U value of 1.13 (+0.8–0.45).

The calculated U values and errors for the tree models M3, M4 and M5 were 1.25, 0.85 and $0.97+0.15/-0.13$ Wm^{-1} K^{-1}, and for M6, it was $0.99+0.32/-0.27$ Wm^{-1} K^{-1}.

The enclosure temperature sensors were calibrated against the ambient sensors to a standard deviation of ±0.25 °C. The data for the last hour of measurement was collated ($N\approx360$); thus, the accuracy of the measured temperature rise from ambient was ±0.5 °C and the heat flow per unit temperature rise per metre was less than ±7 % for foam models M3, M4 and M5, and ±11 % for M6.

A lumped enclosure thermal conductance ($\Lambda_{\text{enclosure}}$) for each enclosure was determined by averaging the thermal conductance (Λ_{h}) at each of the sensors, at the heights from the enclosure roof that would be occupied in the enclosure in winter, i.e. the full height of a hive and the top 200 mm of a tree cavity. This was then compared with the calculated U value. Examples of Λ_{h} are shown for W1, M3, M4 and M5 in Fig. 2. In addition, for three typical winter colony masses of 0.6, 1.7 and 2.0 kg, the MCR was tabulated (Table 2). The value of 1.7 kg was cited as a suggested wintering colony mass with an average of 1.6 kg in West Germany (Southwick 1985). In the UK, an average value used in a large scale trial was 1.45 ± 0.4 with a recommended maximum of 1.8 kg (Free and Racey 1968). It should be noted that recommended winter colony masses are often substantially larger (3.2 to 4 5 kg) in North America (Furgalau and McCrutcheon 1992).

Table 1 Hives and tree models

| ID	Format	Material	Source	λ (Wm^{-1} K^{-1})	R (mm)	r (mm)	Area (m^2)	Height (mm)
W1	British National	Wood (cedar)	C.E. Mitchell (supplied by Thornes)					
H2	Kenyan top bar hive	Wood (Pine)	D. Pearce					
H3	Warre (square)	Wood	J. Haverson					
H4	Warre (octagonal)	Wood	J. Haverson					
H5	Skep	Straw and dung	J. Haverson					
H6	British National	EPS	C.E. Mitchell (supplied by Modern Beekeeping, Ltd., manufactured by Paradise Honey Finland)					
H7	British National (2012 design)	EPS	Y. Hunt (supplied by Paynes Southdown Bee Farms, Ltd.)					
H8	British National	EPS	British Hive Supplies, Ltd.					
H10	Langstroth	EPS	Modern beekeeping (manufactured by Paradise Honey Finland)					
H11	Langstroth	EPS	Paynes Southdown Bee Farms, Ltd. (manufactured by Swienty Sønderborg Denmark)					
H14	British National	EPS	Swienty Sønderborg Denmark					
N1	British National Nucleus (1/2 size hive)	EPS	Paynes Southdown Bee Farms, Ltd.					
M3	Hexagonal tube	PIR foam	Custom construction	0.022±5 %	167.5±1	147.5±1	0.075	600
M4	Hexagonal tube	PIR foam	Custom construction	0.022±5 %	117.5±1	97.5±1	0.033	600
M5	Hexagonal tube	PIR foam	Custom construction	0.022±5 %	132.5±1	112.5±1	0.044	1000
M6	1/5 scale cylinder	Small debarked conifer tree	Custom construction	0.12±20 %	44±1	19±1	0.0013	210
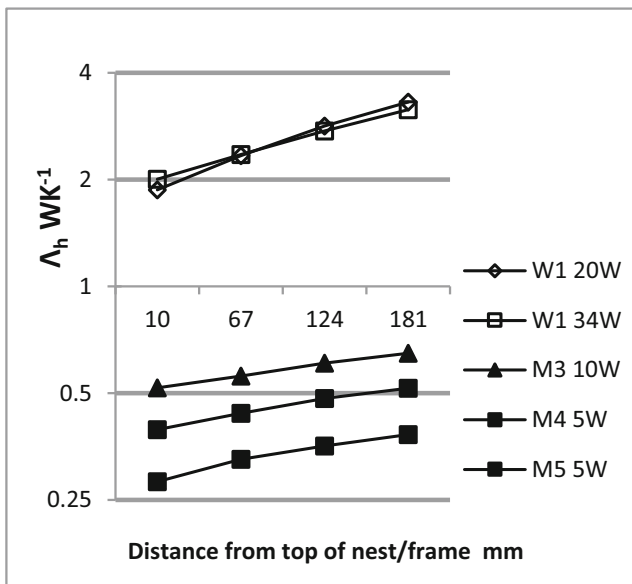
Fig. 2 Enclosure conductance Λ_h versus height from top of cavity for tree models and cedar hive

Fifth scale wood cylinder model M6—foam model validation

This model was included to ensure that the substitution of thin foam for thick wood gave reasonable values for heat transfer. This was achieved using the U value calculated from the shape factors and standard equations (Incropra et al. 2006). In Table 2, we can see that the wood fifth scale model (M6) shows good agreement with the foam models (M3, M4, M5), thus validating the approach of using the U value to size the substitute hexagonal PIR foam models.

Radiation convection

The approach taken assumes that the lumped thermal conductance of the tree material is very much lower than the lumped thermal conductance due to external radiation and convection. This means that changes in the conductance due to changes in external radii between the model and the tree can be ignored. Measurements of the external surface temperatures of the models indicate that this assumption overstates the tree cavity temperature rises by approximately 10 %.

Hive, model and wood λ variation with temperature

PIR, EPS and wood conductivities have similar and small temperature coefficients of 0.46, 0.115 and 0.3 Wm^{-1} K^{-2}, respectively (Bogdan et al. 2005; The Forest Products Laboratory 2010). Thus, the measured temperature range of ~10 °C means that the variation caused by the temperature coefficient would be less than 2 %.

Cavity condition and surrounding wood moisture content

The foam models were constructed from materials with well-controlled uniform properties. However, the wood in both trees and wooden hives is a variable material in that the wood thermal conductivity (λ) can vary as much as 20 % for the

Table 2 Enclosure conductance ($\Lambda_{enclosure}$) and typical winter MCR ($M_{colony}/\Lambda_{enclosure}$)

Hive/tree & heater power	$\Lambda_{enclosure}$ (WK^{-1})	Spread ± (%)	Standard deviation ± (%)	$M_{colony}/\Lambda_{enclosure}$ (kg W^{-1} K)		
				Colony mass (kg) 0.6	1.7	2
H10 20 W	1.30	18	7.5	0.46	1.30	1.53
H11 20 W	0.98	13	6.6	0.61	1.73	2.04
H14 20 W	0.97	14	6.8	0.62	1.75	2.05
H2 20 W	1.59	28	8.1	0.38	1.07	1.26
H3 20 W	1.28	35	6.4	0.47	1.33	1.56
H4 20 W	1.31	26	8.3	0.46	1.29	1.52
H5 20 W	0.97	22	6.0	0.62	1.76	2.07
H6 20 W	1.31	16	7.6	0.46	1.30	1.53
H7 20 W	1.22	11	10.0	0.49	1.39	1.64
H8 20 W	0.91	14	6.5	0.66	1.86	2.19
M3 10 W	0.58	11	6.4	1.03	2.91	3.43
M4 5 W	0.34	15	7.0	1.78	5.06	5.95
M5 10 W	0.49	13	6.2	1.23	3.48	4.09
M6 1.5 W	0.52	0	11.7	1.16	3.29	3.87
N1 20 W	0.75	11	6.1	0.80	2.27	2.67
W1 20 W	2.59	28	8.3	0.23	0.66	0.77
W1 34 W	2.56	22	8.2	0.23	0.66	0.78

same species at the same water content and density (this variation has been taken into account). Moreover, the water content of the wood surrounding the nest cavity is unknown and water content is a considerable factor in determining the λ value. If we assume the water content and density are the same as freshly felled wood, then λ may be twice as large as the values used (The Forest Products Laboratory 2010).

The action of the honeybees in supplying drying heat to the wood surrounding the cavity, the decayed condition of the inner layers of the wood providing an air-filled foam and the presence of bark and cambium decrease λ.

Therefore, further work is needed to determine a distribution of λ to a higher confidence.

Discussion

Ratio of colony mass to lumped enclosure conductance, metabolic rates and clustering

Clustering in honeybee colonies is where the individual honeybees pack closely together in response to low nest air temperatures or behavioural cues (Seeley 1985). Southwick (1982) characterised the temperatures and metabolic rates for honeybee colonies (*A. mellifera ligustica*) in near isothermal nest conditions, i.e. the nest ventilated with fixed temperature air. He showed that the metabolic rate ($q_{metabolic}$) for whole colonies reached an un-clustered maximum of 20 Wkg^{-1} at a ventilated temperature of 20 °C, and on cooling, it reached the clustered minimum with 5 Wkg^{-1} at 10 °C, and also how it was independent of colony mass, provided that the mass was greater than 0.2 kg. To relate this to a realistic non-isothermal nest with an enclosure, we need to consider the heat transfer equation, where the metabolic heat of the colony ($M_{colony} \times q_{metabolic}$) is equal to the $\Lambda_{enclosure}$ multiplied by the air temperature difference across the enclosure walls ($T_{external} - T_{nest}$). Equation 1, for a given nest temperature and its metabolic rate, shows the relationship between external temperature ($T_{external}$) and the ratio of colony mass to lumped enclosure thermal conductance ($\left(\frac{M_{colony}}{\Lambda_{enclosure}}\right)$) i.e. MCR.

The values from Southwick (1982) for the T_{nest} 20 and 10 °C metabolic rates and Eq. 1 are used to plot values of $T_{external}$ against MCR as shown in Fig. 3.

$$T_{external} = T_{nest} - q_{metabolic} \frac{M_{colony}}{\Lambda_{enclosure}} \qquad (1)$$

Onset of clustering, validation of MCR and predictions

From Fig. 3 and using the results for MCR in Table 2, the predicted value of $T_{external}$ at the onset of clustering ($T_{nest} \approx$
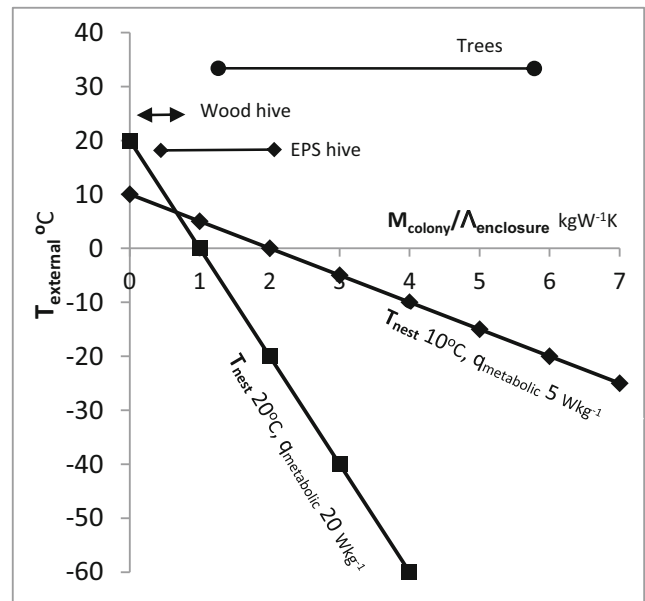

Fig. 3 MCR versus $T_{external}$ for key nest temperatures

20 °C), in conventional hives (W1), is in the expected and commonly observed range of 15 to 5 °C. However, for EPS (H6, H7, H8, H10, H11 and H14) hives, the predicted onset of clustering is below −20 °C. The predicted $T_{external}$ at the onset of clustering in trees is at considerably lower external temperatures, even for small colonies. For example, at MCR= 4 kgW^{-1} K, the onset of clustering will occur at external temperatures of −60 °C.

Inner nest thermal homeostasis and clustering hysteresis

In order to maintain a core thermal homeostasis in isothermal conditions, as the nest surface temperature rises above 10 °C, the colony starts to come out of cluster. When nest surface temperatures fall below 20 °C, the colony begins to cluster, i.e. without hysteresis. Looking at Fig. 3, we can see that the T_{nest} 10 °C line and the T_{nest} 20 °C cross at MCR are ≈0.7. This implies that honeybees will go into cluster at a much lower temperature than they will come out of cluster at MCR values above 0.7. From Table 2, we can see that conventional wooden hives (W1) have MCR values of 0.8 or less. Thus, we can infer that colonies in these hives cluster and un-cluster with little hysteresis. In contrast, we might expect colonies with MCR >>0.7 kgW^{-1} K to cluster and un-cluster with considerable hysteresis.

The biological consequences are that for high MCR enclosures such as trees, honeybees will maintain mobility well into winter. However, should the honeybees be provoked to cluster by extreme weather or long periods of darkness, it will take significantly warmer weather outside the enclosure to break the cluster. This behaviour is well suited to coping with long-lasting extreme events by ensuring that the bees do not start to

expend energy at higher rates until good weather has been well established. However, it should be recognised that the high heat capacity of the tree enclosures will also greatly increase hysteresis as the bees will be storing significant amounts of energy in the fabric of the tree. This is a topic for further research.

Reduction of nest humidity homeostasis energy cost

In enclosures, with entrances only in the lower part, the buoyancy of water vapour in dry air and the generation of heat and water vapour from honeybee metabolism ensure that the nest humidity is limited by the temperature and vapour permeability of the enclosure walls. The honeybees coat the inside of the enclosure with propolis derived from tree resins (Seeley 1985) which have very low water vapour permeability (Hagenmaier and Shaw 1992) and form a vapour barrier. This implies an accumulation of water vapour in the top of the nest limited only by the enclosure wall temperature. For example, wall temperatures of 30 °C would enable a nest relative humidity (RH) of 90 % at 34 °C. Previous workers in this field, with *Apis mellifera scutellata* (Human et al. 2006), have overlooked the dehumidification effect of the condensing, cool surface of the high conductance walls. Their low results of typically 40 % RH may be explained by air with water vapour at 34 °C, condensing on a hive wall at its dew point temperature of circa 19 °C (Lawrence 2005).

To overcome this, dehumidification effect requires continual expenditure of considerable energy (2.2 MJ kg^{-1}) in evaporating the water to replace the vapour continually condensing on the walls and/or preventing air circulation close to the enclosure walls. This high energy cost may explain the weak humidity regulation observed by researchers (Human et al. 2006). This is in contrast with the energy required to regulate humidity in a nest with low conductance walls where the wall temperature rises to 30 °C near the brood nest and is lower in other parts of the nest. As described above, the humidity in the air surrounding the nest will rise to circa 90 % RH. Regulation to lower humidity can then be achieved by circulation of the air into the parts of the nest where the walls are cooler. In this case, the latent heat released by condensation is contained within the nest. The net energy required is only that necessary to heat air from the required RH and dew point, back to 34 °C, which is less than the latent heat released by condensation. High MCR enclosures, by reducing the energy expenditure in humidity control and enabling other humidity control mechanisms, may reveal more honeybee humidity control behaviours.

Implications for *Varroa destructor*

Kraus and Velthuis (1997), investigating the causes for lower varroa (*V. destructor*) breeding success in the tropics (de Jong et al. 1984), described that in three test series with a total of 127 brood cells kept at 79–85 % RH on average, only 2 % of the mites produced offspring, whereas with a total of 174 brood cells kept at 59–68 % RH on average, 53 % of the mites produced offspring. This demonstrated that high nest humidity results in very poor varroa breeding success. In contrast, higher humidity has been shown to improve survival in *Apis mellifera carnica* and *A. mellifera jemenitica* (Hossam 2012) and improves egg viability (Doull 1976). It has been shown to be only a minor factor in chalkbrood disease (*Ascophaera apis*), with an effect of an order of magnitude less than a lowered temperature (Flores 2011), indicating that a highly insulated nest with high humidity would result in markedly reduced chalkbrood incidence but not its elimination.

Huang (2012) has also observed the varroa breeding failure phenomenon and commented "If there are ways to artificially increase the hive RH to about 80 %, then the varroa mite population will never increase to a damaging level".

From the discussion above, we can see that, with a high MCR, very high nest humidity can occur in the air surrounding the nest at normal brood temperatures, in cool external conditions (e.g. MCR ~4, $T_{external}$ ~10 °C) and does not require the external tropical conditions Kraus and Velthuis referred to in their discussion. The build-up of humidity in an enclosure with a vapour barrier at low conductance has been experimentally demonstrated in passive-house building research (Mlakar and Štrancar 2013).

The implication is that high humidity, as a practical means to control varroa, is now a valid topic of research.

Unexpected results for top bar hives and dung-covered skep

These hives gave lower conductance results than may be first assumed, but on closer inspection, this can be explained by the differences in thickness, conductivity and geometry of the material employed in the construction. This is particularly so for the dung-covered skep, which ranked among the lowest conductance hives. This is due to the material's conductance, its thickness and the tapering top, which exploits the fact that conductance is determined by the logarithm of ratio of the inner and outer radii. This effect will also be present in the tapering irregular top of real tree cavities and enable even lower conductances to be realised in that space, which is a subject for further research.

Relevance to other frame and box hive designs

This study investigated British National wood and EPS as well as Langstroth EPS designs. There are a number of wooden box hive designs in use that are very similar to the British National, e.g. Dadant, Langstroth and Commercial, in those characteristics that determine thermal conductance, i.e. roof

surface area, overall surface area, wall and roof thickness, materials and construction. For example, the British National has a roof surface area of 0.212 m^2, compared to 0.211 and 0.210 m^2 for the Langstroth and Dadant hives (Cushman 2011). It is also marginally smaller in overall surface area of 0.626 m^2, compared to 0.657 and 0.657 m^2. The example tested was constructed from Western Red Cedar (*Thuja plicata*), the lowest conductivity wood (The Forest Products Laboratory 2010) in common hive construction, and therefore, will be similar in conductance to Langstroth and Dadant hives constructed of that wood and thickness (19 mm). EPS designs are not as uniform in construction and materials, and thus, this research concentrated on EPS hives. Investigation into the detailed performance differences of various floor, ventilation and roof features is left as a subject for future research.

Research protocol recommendations

Adoption of MCR as a comparative survival factor

By rearranging Eq. 1, we can see that MCR is inversely proportional to the heat loss per honeybee per degree centigrade of temperature difference between the inside and outside of the enclosure, i.e. WK^{-1} bee^{-1}. Thus, the MCR is inversely proportional to the thermal stress on the honeybees in the nest, which their various coping behaviours must overcome. It should be noted that stress is named as a key factor in various honeybee parasites and diseases (Mayack and Naug 2008; Even et al. 2012).

While it has been noted that changing colony size and insulation can affect survival (Guzman-Novoa et al. 2010; Villumstad 1974), most of the formal studies have either omitted the colony mass or the numeric value of nest enclosure conductance or have not mentioned the entrance size and the presence or absence of top vents (which can negate the effect of insulation). As a result, it has led to confusion and inconsistency in results between the researchers and apiculturists. MCR combines both factors in a consistent quantitative manner, with a firm analytical foundation. Including the measurement of MCR as part of the experimental protocol, as well as the external temperature, will allow researchers to correlate the honeybee energy stress levels from one experimental environment to another.

More realistic thermal environment

For researchers wishing to understand the behaviour where the honeybees have greater control of their temperature, humidity and heat expenditure and may exhibit more energetic behaviours, this research indicates that the honeybees should be placed in a nest with shape and insulating material that yields a $\varLambda_{enclosure}$ of 0.5 WK^{-1}, a value equivalent to a typical

tree enclosure. The colony should also have sufficient mass to generate a MCR value that will place the colony well into the region of clustering hysteresis, i.e. 2 kgW^{-1} K or greater.

Conclusions

There is clearly a substantial difference in the heat transfer characteristics between the natural enclosures of honeybees and man-made hives. The resulting changes in the temperature and humidity in the air inside the enclosure, surrounding the nest, can have a profound effect on the well-being and behaviour of the honeybees that inhabit it. Depending on relative water content of the enclosure material, the difference in heat transfer may be as large as a factor of 4 to 7 times for wooden hives and 1.5 to 5 times for full-size expanded polystyrene hives (Fig. 2, Table 2) compared to tree enclosures.

The energy expended within the nest maintaining homeostasis of temperature and humidity is governed by the fundamental physical principle of the conservation of heat and mass. Quantitative knowledge of heat transfer from the nest to the outside environment through the enclosure is therefore essential to the understanding of homeostasis and other energy-intensive behaviours such as honey ripening. The quantity, a colony mass-to-thermal conductance ratio of the enclosure, fills in a missing piece in the understanding of the heat transfer from the honeybee nest and related processes.

The debate over insulation and colony size in apiculture dates back to at least mid-nineteenth century. This study provides a quantitative foundation for that continuing debate.

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